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The Crane Fly Genus *Dolichopeza* in North America

BY

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TABLE OF CONTENTS

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* This work was done primarily while the author was in the Division of Insects, University of Michigan Museum of Zoology, Ann Arbor, Michigan.

INTRODUCTION

A hundred years have passed since Charles Darwin, in *Origin of Species,* wrote: "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera." During that century, repeated observations on various groups of organisms—vertebrate and invertebrate animals, as well as plants—have supported Darwin's belief, and these observations have been summarized in statements known as Jordan's Law and, more recently, Gause's Principle. Closely related species and races will by reason of their common origin inhabit ranges in proximity to each other. Competition between these species in areas where their ranges overlap is calculated to result in the survival of one and destruction or displacement of the others. The consequences of such competition are described in a statement of Jordan's Law by Hubbell (1936: 518-519): "In any group of allied forms, whether species or races, the most closely allied will be found not in the same territory and habitat, nor in widely separated regions, but either in adjacent areas separated by a barrier of some sort, or if in the same area then in different but not entirely unrelated or dissimilar ecological situations."

Because this expectation is so completely reasonable, instances of nonconformity with it are of unusual interest. Such an instance is found in the crane fly genus *Dolichopeza,* it having been the experience of collectors that wherever they took one species of the genus they nearly always collected at least one other. In fact, at one time, in a certain favorable habitat, I captured no less than six species of *Dolichopeza* in a single sweep of my net!

As organisms usually conform to our well-founded generalizations, one tends to regard the case of *Dolichopeza* with suspicion. If we have interpreted the genus correctly, its species must be reasonably closely related; the fact is that certain groups among North American *Dolichopeza* comprise pairs or larger aggregations of sibling species, the forms so nearly alike that they may be distinguished only by microscopic details, in many cases. But it might be that the species are ecologically separated in some way as to preclude competition. Or, in view of the existence of groups of sympatric "sibling species," perhaps many of the recognized forms are really not species at all but merely polymorphic phenotypes of one or a few species.

The following study was undertaken partly to try to learn which of the described forms actually are species. This required extensive laboratory rearing, field observation and detailed study and interpretation of variation. It was the further purpose of this investigation to find how the species are related to each other, structurally and ecologically. This involved some study of comparative anatomy of both adults and immature stages, and again detailed field observations. Lastly, an answer was sought to the question: if there are closely related species living together in the same habitat, as has appeared to be the situation, how is it that one has not eliminated the others through competition?

Earlier North American workers on the Tipulidae have quite naturally concentrated their efforts on exploration of the fauna, which is still not completely known, even on the basis of the adult flies. Because of the relatively minor economic importance of crane flies, there has been no pressing need for studies of their biology; accordingly, the few earlier detailed accounts of North American tipulids have dealt usually with only one species or a scattering of species within a large genus. The following study, in contrast, attempts to present a more coherent picture, bringing together all available data on every species of the genus *Dolichopeza* known to occur in North America.

In gathering these data, it soon became evident that nearly every aspect of the biology of *Dolichopeza* was either uncertain or unknown. Geographical ranges were only sketchily outlined, only fragmentary information was available on the immature stages of but a single species, nothing was known of the internal morphology of either adults or immatures, and the habitats of these stages had not been specifically defined. This investigation therefore expanded into a search for whatever could be learned about the genus *Dolichopeza,* with the idea that answers to the problems posed above might be found in diverse places.

ACKNOWLEDGMENTS

If I were to place a note of dedication in the front of this work, that dedication would be to the late Professor J. Speed Rogers, former Director of the University of Michigan Museum of Zoology, for it was Dr. Rogers who encouraged me to undertake this study and who got me interested in crane flies in the first place. As a teacher, he was always enthusiastically interested in the progress of his students and ever ready with encouragement. He placed at my disposal his entire accumulation of *Dolichopeza,* a collection larger than all others in the world combined, but what was more important he impressed me with the desirability—in fact, the need—of supplementing laboratory observations by the study of living crane flies in their natural environments. He was a cautious and careful worker, maybe even meticulous, and he would not like to see a conclusion reached unless every available shred of evidence had been closely examined. While I cannot measure up to his ideals, it is my hope that the work which follows would have pleased him.

My sincerest thanks go to Professor Theodore H. Hubbell, now Director of the University of Michigan Museum of Zoology, for reading most of this paper in its early stages and offering many valuable suggestions, often in the form of thought-provoking questions. His advice and encouragement have been of immeasurable help.

Dr. Charles P. Alexander, distinguished student of the world fauna of Tipulidae, generously provided me with his collection records of *Dolichopeza* and allowed me to inspect, in his personal collection at Amherst, Massachusetts, the types and other specimens of North American and exotic species. I am indebted to Dr. Alexander for this invaluable aid and for his having constructed much of the foundation upon which this investigation is based.

For permission to do intensive collecting in various state parks in Indiana and for the courteous co-operation shown by park personnel, I wish to thank the Department of Conservation of the state of Indiana. Recognition is also due Dr. Irving Cantrall for per-

mission to do concentrated collecting on the University of Michigan's Edwin S. George Reserve.

Data on distribution and intraspecific variation have been considerably increased through the generous co-operation of several individuals and institutions. Dr. Joseph Bequaert made available types and other material in the Museum of Comparative Zoology at Harvard University; the collection of the United States National Museum was loaned by Dr. Alan Stone, and Dr. J. R. Vockeroth sent specimens from the National Museum of Canada. Others who made valuable contributions include Dr. Edward L. Kessel of the California Academy of Sciences, Dr. Jean Laffoon of Iowa State College, Mr. Peder Nielsen of Silkeborg, Denmark, Dr. E. F. Cook of the University of Minnesota, Dr. F. N. Young of Indiana University, Mr. J. A. Wilcox of the New York State Museum, Dr. W. V. Balduf of the University of Illinois; and the entomological staffs of the Illinois State Natural History Survey, the Academy of Natural Sciences of Philadelphia, the American Museum of Natural History, Pennsylvania State University, the Milwaukee Public Museum, and the University of Kansas, who generously allowed me to examine collections in those institutions during my visits there.

I gratefully acknowledge the co-operation of Dr. William C. Steere, who made the more difficult determinations of bryophytes. Other materials incidentally associated with this research were identified by Dr. W. J. Gertsch of the American Museum of Natural History, Mr. Sherman Moore of Detroit, and Dr. C. F. W. Muesebeck, Dr. B. D. Burks, Mr. H. W. Capps and Miss L. M. Walkley of the United States National Museum. To the many others whose help made this work easier I offer my sincerest thanks. Permission to use portions of maps of North America from the Hall's Outline Series, by Dr. Robert B. Hall, has been granted by the Department of Geography of the University of Michigan.

THE GENUS *DOLICHOPEZA*

Including nearly a hundred and seventy recognized forms in nine subgenera, the genus *Dolichopeza* comprises a varied and extremely widespread assemblage of species, some of which are not markedly different from certain species of other tipuline genera. By reason of possible future changes in generic definition, species or even subgenera of the present-day genus *Dolichopeza* may eventually be assigned to other genera. The recognized subgenera, however, are clearly related and, in general, seem to be natural groups of species. *Dolichopeza* includes those tipuline crane-flies which have extremely long legs and feet, the wing vein R_{1+2} ordinarily absent or atrophied, the rostral nasus small or lacking, and the radial sector of the wing usually short and nearly traverse. Certain of these characteristics, of course, are shared by other genera, and some are not true of all *Dolichopeza.* The major subgenera may be separated by characters set forth in a key by Alexander (1931b). They are: *Dolichopeza* Curtis, *Nesopeza* Alexander, *Mitopeza* Edwards, *Oropeza* Needham, *Trichodolichopeza* Alexander, and *Megistomastix* Alexander. In recent years, three additional subgenera, embracing only a few species, have been described by Alexander. These are: *Afrodolichopeza, Hovapeza,* and *Sinoropeza.*

Excepting South America and the Antarctic, all the major land masses of the world have some members of *Dolichopeza* in their insect faunas, and it may be that later exploration along the western highlands of South America will prove the genus to be also present there. The typical subgenus is the most widespread, represented by two species in North America, by four in Europe, five in Africa and Madagascar, eight in southern and eastern Asia, and thirty-five species in Australia and New Zealand. The only other subgenus bridging a major geographical gap is *Oropeza,* of which there are nine species known from eastern Asia (Japan, China, Korea, Formosa, and India) and thirteen from North America. Sixty-four species of *Nesopeza* are recognized, of which all are Asiatic and nearly all concentrated in southeastern Asia. There are ten species of *Trichodolichopeza* known from east-central to south Africa, and eight species of *Megistomastix,* found only in the West Indies. *Afrodolichopeza* includes a half-dozen species from east-central Africa; *Sinoropeza* comprises two species from southeastern Asia; and *Hovapeza* is known from a single species from Madagascar.

NORTH AMERICAN *DOLICHOPEZA*

This study is limited to the species of the subgenera *Dolichopeza* and *Oropeza* that occur upon the mainland of North America. Although few of the hundreds of species of Tipulidae inhabiting this continent are likely to be confused with *Dolichopeza,* it would be well, at the outset, to distinguish the genus from its nearer relatives. In having the terminal segment of the maxillary palpus very much elongated, the antennae with twelve or thirteen segments, the vein Sc_1 normally absent, and the cubitus with a deflected angle at cross-vein m-cu, *Dolichopeza* is included in the subfamily Tipulinae and is excluded from the Limoniinae, some of which have a superficially similar general appearance. Among North American Tipulinae, only three genera have extremely long and slender legs, with the tarsus exceeding in length the femur and tibia together. Of these, *Brachypremna* and *Megistocera*, both of which are essentially southern in distribution, may at once be distinguished from *Dolichopeza* by their having a nasus on the rostrum, the vein R_{1+2} present, and the antennae quite short, approximately the length of the head. The species of *Tipula* and *Nephrotoma* that resemble *Dolichopeza* may likewise be separated by the presence of vein R_{1+2} and, in *Tipula*, by the obliqueness of the radial sector.

The wings of *Oropeza*, as of the Tipulinae generally, are characterized by the presence of the cell 1st M_2 (Fig. 1), while this cell is not found in the two North American species of the subgenus *Dolichopeza* (Fig. 2). The cross-vein m-cu joins the media beyond its fork in subgenus *Oropeza* but before the first fork of the media in *Dolichopeza*. Other lesser points of difference will be discussed later.

Immature stages of both subgenera of *Dolichopeza* closely resemble those of *Tipula*, although both larvae and pupae of *Oropeza* may be distinguished by the presence on the sides of the eighth abdominal segment of two blunt, conical lobes. I have not made any comparative study of the eggs of various tipuline genera. Detailed comparisons of the larvae and pupae of *Dolichopeza* with those of its nearer relatives will be made in the sections on the morphology of those stages.

There are at the present time sixteen species and one subspecies of North American *Dolichopeza* recognized in the literature. They are *Dolichopeza* (*Dolichopeza*) *americana* Needham, *D.* (*Oropeza*) *carolus* Alexander, *D.* (*O.*) *dakota* Alexander, *D.* (*O.*) *dorsalis* (Johnson), *D.* (*O.*) *dorsalis rogersi* (Alexander), *D.* (*O.*) *johnsonella* (Alexander), *D.* (*O.*) *obscura* (Johnson), *D.* (*O.*) *polita* (Johnson), *D.* (*O.*) *pratti* Alexander, *D.* (*O.*) *sayi* (Johnson), *D.* (*O.*) *sessilis* Alexander, *D.* (*O.*) *similis* (Johnson), *D.* (*O.*) *subalbipes* (Johnson), *D.* (*O.*) *subvenosa* Alexander, *D.* (*O.*) *tridenticulata* Alexander, *D.* (*O.*) *venosa* (Johnson), and *D.* (*O.*) *walleyi* (Alexander).

Of these, thirteen appear to be valid species: *americana, carolus, dorsalis, johnsonella, obscura, polita, sayi, similis, subalbipes, subvenosa, tridenticulata, venosa* and *walleyi*. I consider *Dolichopeza pratti* to be a subspecies of *polita*, *dakota* a synonym of *walleyi*, and *sessilis* and *dorsalis rogersi* synonyms of *dorsalis.* Support for the opinions expressed here will be found in the treatments of the individual species involved. One new species in the subgenus *Dolichopeza* and a new species and one additional race of *polita* in *Oropeza* are described and named in this revision.

In addition to the venational distinction between the subgenera mentioned earlier, a further convenient division of the genus may be made on the basis of the gonapophyses of the male hypopygium (Fig. 3). As the male of the one new species of subgenus *Dolichopeza* is unknown, *D. americana* is in a class by itself, in this regard. Five of the other species have the gonopophyses in the form of small knobs, densely covered at the tip by stout, black, curved spines. This group includes *johnsonella, obscura, polita, subalbipes,* and *tridenticulata,* and one new species; it will be referred to hereinafter as the *obscura* group. In the remaining species, the gonopophyses are generally flattened and blade-like, variously tipped, and without the abundant black spines of the *obscura* group. These constitute the *sayi* group, which includes *carolus, dorsalis, sayi, similis, subvenosa, venosa* and *walleyi.* Gonapophyses of representative species of these groups are compared in figures 4 through 7.

The genus may also be subdivided into two major color groupings: those species that are of a dusky brown coloration (*americana, johnsonella, obscura, polita,* and *tridenticulata*) and those which are chiefly yellowish or buffy and marked with darker spots and stripes, especially in the form of prescutal stripes and pleural spots on the thorax and dark annulations on the abdomen. The darkly colored species are most often found associated with deep shade, in either rock-gorge or wooded situations, while the paler forms are more characteristic of less intensely shaded, often sparsely sun-flecked vegetation. These circumstances, of course, invite speculation about the selective advantage of coloration in *Dolichopeza.*

HISTORICAL REVIEW

The genus *Dolichopeza* was established by John Curtis in 1825 to include the one known European species, which he named *Dolichopeza sylvicola* (Curtis, 1825: Plate 62.)* This species had already been described as *Tipula albipes* by Ström in 1768.

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* Curtis' *British Entomology* is a series of colored plates, 770 in all, accompanied by descriptive notes. Published in London, these plates were issued a few each month from 1823 to 1840.

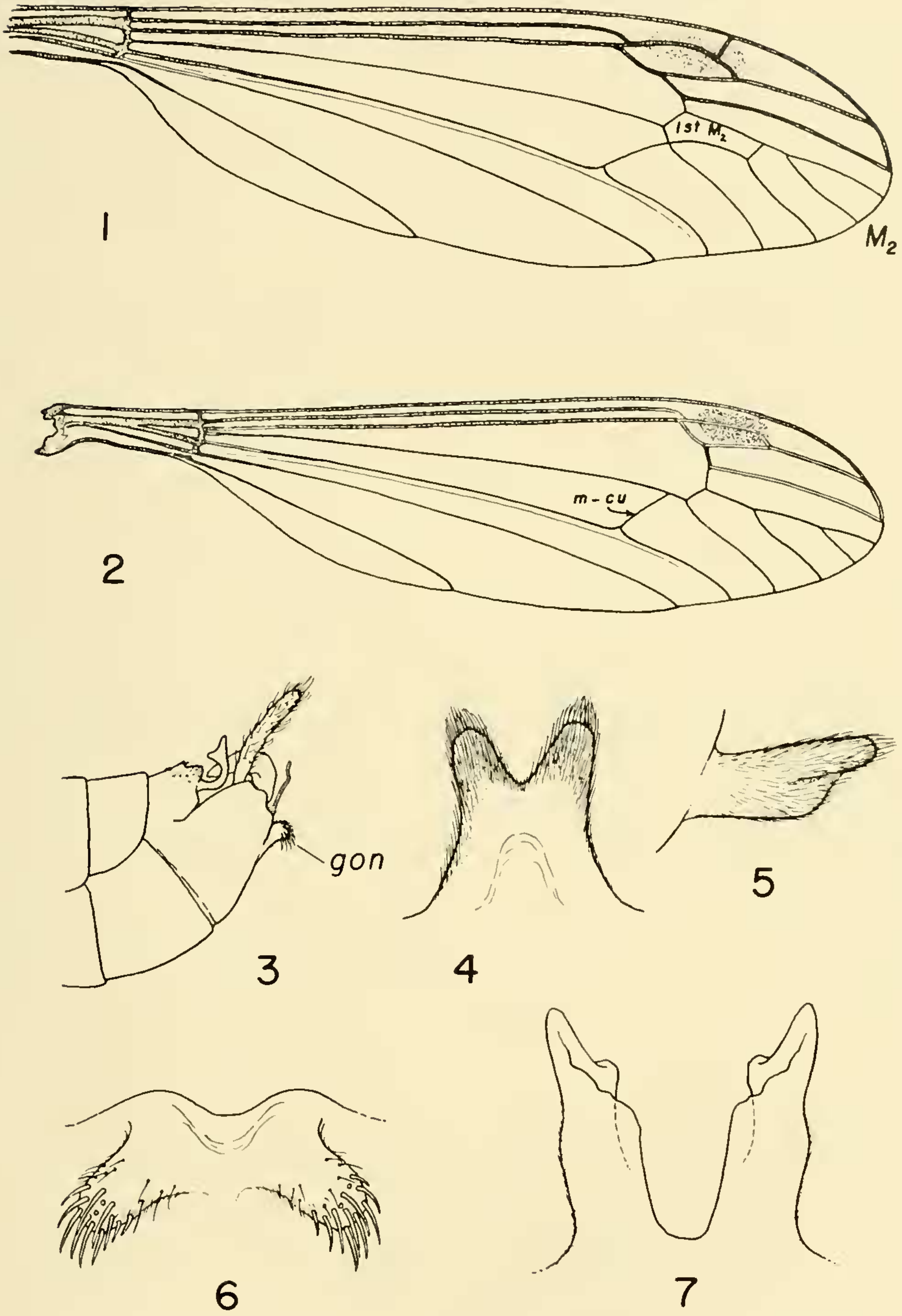

FIG. 1. Wing of *Dolichopeza (Oropeza) tridenticulata,* showing cell 1st M_2 or discal cell. FIG. 2. Wing of *Dolichopeza (Dolichopeza) americana,* showing position of m-cu cross-vein relative to first branching of M. FIG. 3. Hypopygium of *Dolichopeza (Oropeza) obscura,* male, left lateral aspect; gon—gonapophysis. FIG. 4. Gonapophyses of *Dolichopeza (Dolichopeza) americana,* dorsal aspect. FIG. 5. Same as 4, left lateral aspect. FIG. 6. Gonapophyses of *Dolichopeza (Oropeza) obscura,* postero-ventral aspect. FIG. 7. Gonapophyses of *Dolichopeza (Oropeza) sayi,* postero-ventral aspect.

Accordingly, the type species is *Dolichopeza albipes* (Ström). America's great pioneer entomologist, Thomas Say, in 1823 described *Tipula annulata* (Say, 1823: 25), the description of which is now thought to pertain to a species of *Dolichopeza.* Unable to locate the specimens upon which Say based his description, I must assume any types were lost at the time most of the Say collection was destroyed by dermestid beetles, in Philadelphia, about 1840 (Weiss and Ziegler, 1931: 203-212.)

Actually, it is uncertain that what Say described was a *Dolichopeza;* the description is quite brief and rather general in its wording. However, sometime between 1823 and 1828, specimens thought to be *Tipula annulata* Say reached C. R. W. Wiedemann in Austria, and in 1828 he noted that both male and female of this species were represented in his collection (Wiedemann, 1828:54). I have examined these specimens (now in the Naturhistorisches Museum in Vienna), which are two males and a female of *Dolichopeza* (*Oropeza*) *johnsonella* and two males of a species of *Tipula.* That these were determined by Wiedemann (they are so labelled) suggests they had not been compared with any specimens in America but were merely identified by comparison with Say's written description of *Tipula annulata.*

Fifty years later, C. R. Osten Sacken (1878: 40) placed *Tipula annulata* provisionally in *Dolichopeza,* noting that ". . . the forceps of the male has a different structure, etc." Seven specimens of *Dolichopeza* spp., labelled "*Dolichopeza annulata* Say?" (probably in Osten Sacken's handwriting) are to be found in a tray marked "Loew and Osten Sacken" in the Museum of Comparative Zoology at Harvard University. Osten Sacken's catalogue indicates that specimens of what he called *Dolichopeza annulata* were located in that museum. It would appear that Osten Sacken, like Wiedemann, decided after reading Say's description that certain North American tipulids in his collection were the species in question. It was Osten Sacken, however, who first critically compared North American *Dolichopeza* with *Tipula.*

Dr. James G. Needham, in 1908, described a new species, *Dolichopeza americana,* which he recognized as a true *Dolichopeza,* and also established the genus *Oropeza* to include a structurally similar American species in which the cell 1st M_2 is present in the wing. It seems that Needham, too, made an independent decision as to the identity of Say's *Tipula annulata,* for after having collected certain specimens which he so identified, he made *Tipula annulata* the type species of *Oropeza.* It was not long after Needham's work that the actual diversity of North American *Dolichopeza* became known, through the investigations of Mr. Charles W. Johnson of Boston. In his "New and Little Known Tipulidae," published in 1909, Johnson described seven new forms and redescribed *Oropeza annulata*, assigning it the name *Oropeza sayi.* (Say had not been aware that Linnaeus had, in 1758, given the name *Tipula annulata* to the crane fly now known as *Limonia annulata.*) Johnson recognized as new species: *Oropeza similis, O. dorsalis, O. venosa, O. albipes, O. subalbipes,* and *O. obscura,* and a form *polita* as a variety of *obscura.* The individual histories of these, as well as of the other species listed in this summary, are treated under their separate titles.

All rearrangements and descriptions of species of North American *Dolichopeza* published since Johnson's paper have been the work of Dr. Charles P. Alexander. Arranged chronologically, they are: 1922—*Oropeza rogersi;* 1930—*Oropeza johnsonella;* 1931—*Oropeza walleyi* described and Johnson's variety *polita* raised to full species rank; 1931—the genera *Oropeza* Needham and *Dolichopeza* Curtis merged, together with other genera, into the genus *Dolichopeza,** as subgenera (Alexander, 1931b: 269); 1931—*Dolichopeza* (*O.*) *tridenticulata;* 1940—*Dolichopeza* (*O.*) *subvenosa;* 1941—*Dolichopeza* (*O.*) *pratti* and *D.* (*O.*) *sessilis;* 1942—*Dolichopeza* (*O.*) *albipes* renamed *D.* (*O.*) *carolus,* since, through his action of 1931, he had made *Oropeza albipes* Johnson a homonym of *Dolichopeza albipes* (Ström), of Europe; 1942—*Dolichopeza* (*O.*) *rogersi* reduced to subspecific rank; and 1944—*Dolichopeza* (*O.*) *dakota* described.

The biology of North American *Dolichopeza* has been given brief treatment by Alexander in "The Crane Flies of New York" (Part I, 1919; Part II, 1920); and the late Dr. J. Speed Rogers has made several additions to the knowledge of the biology of adult and immature stages in his studies of the Tipulidae of the Cumberland Plateau (Rogers, 1930), of northern Florida (Rogers, 1933), and of the Edwin S. George Reserve, Michigan (Rogers, 1942).

MATERIALS STUDIED

Over 11,300 adult and 600 later stage immature specimens of North American *Dolichopeza* have been examined in the course

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* Johnson (1910:708) had earlier indicated this relationship of the two groups by using the heading "*Oropeza* Needham (*Dolichopeza* Curtis)" above a list of species of *Oropeza.* However, in a later paper (Johnson, 1925:32), he used the name *Dolichopeza americana* and the generic name *Oropeza* for several other species.

of this study. Adult flies were distributed among the various species as follows:

americana—1016
carolus—1150
dorsalis—285
johnsonella—425
obscura—2028
polita sspp.—2150
sayi—257
similis—67
subalbipes—530
subvenosa—138
tridenticulata—2617
venosa—132
walleyi—558
new spp.—31

Eggs of all species have been examined, and first instar larvae were obtained in all instances except *subalbipes, subvenosa, tridenticulata* and the two new species. Later instar larvae were obtained for all species except *carolus, johnsonella, subvenosa* and the new species referred to above; and pupae were found for all but *johnsonella* and the new species.

Of the total number of adults, about 2900 were in the Rogers collection at the University of Michigan, and somewhat over 600 were seen in collections from other individuals and institutions. More than 7800 adults and all but a dozen or so of the immature stages were collected during my field trips in the summers of 1949-1953 and 1957-1958. The types of all species were examined, except *americana* and *sayi*, of which species all type material is lost.

In the study of the natural history of *Dolichopeza*, many hundreds of samples of mosses and hepatics, representing perhaps 200 species, were collected and examined for larvae or pupae. Most of these contained neither, but abundant sampling was necessary, since all bryophytes were suspected habitats, especially at the outset of the search. Many actual habitats certainly would have been overlooked had any other procedure been adopted.

Incidental observations on and collections of plants and animals ecologically related to *Dolichopeza* were made. These observations have been interpreted and the collections identified by various specialists whose contributions are mentioned separately later.

COLLECTION AND PREPARATION OF MATERIAL FOR STUDY

Species of *Dolichopeza* vary in their response to light but are generally negatively phototropic, seeking the deep shade beneath undercut rocks and banks or the green twilight below lush vegetation of marsh borders and swampwoods. Unlike the more active and rapidly flying species of *Tipula* and *Nephrotoma* found in the same general habitats, *Dolichopeza* spends the daylight hours in shaded seclusion and must be hunted in somewhat the way a mammalogist might search for bats in the daytime.

Aggregations of individuals numbering from a few to over 200 may be found in cool, shaded niches in the more favorable forest and ravine habitats. In such cases, many flies may be collected by a single sweep of the net, or the patient collector desiring mating pairs or undamaged specimens may take flies directly into the cyanide jar. Under such conditions, I have collected mating pairs into large, empty jars in order to obtain eggs or observe mating behavior. For flies resting among the roots of wind-thrown trees or in narrow crevices in rock, collection directly into cyanide vials may be the best method, although an alternative is to stir within the cranny with a branch, collecting the flies into the net as they move out. In collecting those species of *Dolichopeza* which are most frequently associated with vegetation of marsh borders and swamps (especially *D. dorsalis* and *D. sayi*), the usual "sweeping" technique is not satisfactory, as it is likely to break the legs off these delicately built crane flies. Rapid trampling of the vegetation will often bring the flies up from their hiding places. In doing this, one should look well ahead, especially for flies crossing small open spaces in the vegetation as they move ahead of the collector. Standing quietly in one place, or moving very slowly, has also proved a profitable method for detecting the movements of these crane flies beneath the cover of plants, and so capturing them. *Dolichopeza sayi, D. similis* and *D. dorsalis* are seldom seen in concentrations and must be taken individually or a few at a time. Other swamp species may be found either dispersed as individuals or gathered into small groups, where some sort of darkened cavity occurs. *Dolichopeza carolus,* usually seen hanging from leafy vegetation in forested ravine habitats, is easily taken by an upward sweep of the net.

To most entomologists, the words "crane flies" at once suggest the legless condition in which these insects are all too often found in collections. That the Tipulidae are fragile certainly cannot be denied, but proper handling will prevent undue loss of legs from most specimens. Correct preparation of specimens begins with their capture. Large cyanide jars are to be avoided; use of smaller vials (30 x 90 mm. shell vials, taped for reinforcement, are very good) prevents breakage of specimens because fewer are placed in one vial, and they have less room to shake around, during and after the killing process. Very shortly after a crane fly is killed in the cyanide vial, it becomes more fragile than when alive. It remains in this rigid but not brittle condition for two to three hours, after which there occurs a period of secondary relaxation, lasting somewhat over an hour. Following this period, dehydration causes increasing brittleness of the insects. To attempt to disentangle and further prepare specimens either during the earlier period of rigidity or after dehydration has become advanced results in great loss of legs, especially in such slender-legged flies as *Dolichopeza* and many species of *Limonia*. During the period of secondary relaxation, however, even the most fragile species may be processed with some speed and without much damage. The flies are placed in paper envelopes (a convenient size is 2 x 3½ inches, No. 2 drug type), upon which the collection data have previously been marked. While still in the relaxed condition, three or four *Dolichopeza*, each with the long legs compactly arranged beneath the body, may be neatly tucked into such an envelope. Warm, dry heat or a calcium chloride desiccator may be used to dry the insects. Specimens prepared in this way arrive in the laboratory undamaged, ready to mount, and accompanied by field data.

Most breakage of tipulids in collections is due to improper mounting. I have never seen a crane fly too large to be conveniently mounted on a point of heavy paper. Flies pressed in envelopes are arranged in one plane, hence are seldom broken during the mounting or labelling processes. Utilization of points cut from two-ply bristol-board for all mounting allows the use of uniformly strong pins (No. 4 are good) and thus prevents damage of specimens due both to attempts to pin through the insect's body and to subsequent pin failure. Dried with the legs folded below the body, flies may be fastened to the point by the left side of the thorax, in such a way that only the one side of the thorax is obscured from view, while the legs receive maximum protection from the point, the pin, and the labels. China cement thinned with ethyl acetate is a very satisfactory mounting material.

In the preparation of labels, the guiding principle should be to make all essential information about the specimen immediately available to other workers who may wish to make use of it, be they in another part of the world or in a different generation or century. Adequate locality data consist of first a major geographical division (state, province, territory, or country, if of small size), then a more limiting designation, a county, district, or reference to a sizeable town, etc., such as is likely to be listed in the indexes to commonly accessible maps. Geographic co-ordinates should be used for little-known areas. References to any but the most widely-known physiographic features is inadequate, as these may not be mentioned in atlases or map indexes. Elevations should always be given for regions of high relief, and specific localities should be mentioned for areas where other environmental factors (vegetation, moisture, etc.) vary greatly. Exact dates are very important, especially in data on groups such as the Tipulidae that are very seasonal in occurrence. Special material (reared specimens, those from which parts have been removed to microscope slides, etc.) should be appropriately labelled. Confusion is certain to occur, sooner or later, if identified insects are not *each* labelled with the proper determination, the authority and the date.

Collection of larvae and pupae is a tedious and time-consuming business, for the immature stages are usually diffusely distributed within their microhabitats. It is practically impossible to obtain eggs or first instar larvae by field collecting methods. About two months after the local peak of late-summer emergence of adults is a good time to gather larvae, if numbers are desired, for the larvae will have grown large enough to be readily seen but will not have been seriously reduced in numbers by predators or severe weather. I believe that predation on the young of the spring generation progresses more rapidly and that the *Dolichopeza* population is thus more quickly reduced.

If fewer individuals but higher percentages of emergence are desired, larvae or pupae should be gathered shortly before the local time for emergence under natural conditions. Most natural mortality will then have occurred, and, given reasonable care in the laboratory, nearly all larvae or pupae will go on to the adult stage. Some hints on the actual places to look for larvae may be found in the discussion of larval habitats. However, an observation of general application is that additional pupae and perhaps larvae are likely to be found in mosses from which pupal skins are projecting, provided that these sites are discovered early in the season of emergence for the species concerned.

Immature stages to be preserved are killed in hot water and stored in 80% alcohol. I have not found it necessary to pass specimens through increasing concentrations of alcohol before storage. Adults stored in alcohol tend to lose their color, although color patterns are often accentuated in the process. Soft structures, both internal and external, retain their shape and are more easily studied in alcoholic material. Large collections of flies may be stored in a small space, in alcohol, although extensive damage to individual specimens will eventually occur, during subsequent handling.

Microscopic preparations used in this study were very simply made. Most materials were soaked in 80% alcohol or warm water until soft, or were first macerated to the desired degree in 7-10%

potassium hydroxide solution and then rinsed in warm water, then transferred directly into polyvinyl alcohol mounting medium.* This substance has good optical qualities, is very inexpensive, and has a slight clearing action that makes the KOH treatment unnecessary in the case of smaller objects. A further advantage is that mounted specimens may be soaked off in hot water and remounted, in case slides become broken or mounts are unsatisfactory. Polyvinyl alcohol, or "PVA" as it is called, has been in use only about fifteen years, so its durability has not been proved.†

METHODS OF STUDY

Adults.—As in any study of a primarily taxonomic nature, this work is based largely upon post-mortem examination of museum specimens, in this case dried and alcohol-preserved flies. However, familiarity with and understanding of a group of organisms come more from studying them in their natural environment. Following insects about to learn what they are up to may seem an idle occupation, in these times when laboratory biology is more the vogue, but particularly in studies involving several closely related, sympatric species, such as is the case with *Dolichopeza*, field observations lead to a better understanding of individual species and may provide the only answers to certain problems of inter-species relationships. Large numbers of living flies were also caged in the laboratory for such purposes as obtaining eggs, observing mating behavior, noting approximate length of life, and other things that could not easily be studied in the natural habitats.

Contraction or deflection of parts of the body in drying, or distention in alcohol, cause inaccuracies and complications in both linear and proportional measurement. For purposes of general description, body length, as used hereinafter, means the straight-line distance from the most anterior part of the head (excluding antennae) to the tip of the abdomen, regardless of the position in which the specimen is preserved. Wing length, the most fixed and easily accessible measurement of adult *Dolichopeza*, is the straight-line distance between the point of attachment and the tip. Even wing length is of little use in describing species, for environmental factors may result in great differences in size within a species. Discussion of preserved adult crane-flies, therefore, will be concerned chiefly with structural characteristics.

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* Polyvinyl alcohol is a plastic prepared from PVA powder (I use DuPont "Elvanol," grade 71-24): sift 20 grams of the powder into 88 cc. of cold water; heat at 85° F. in water bath, stirring constantly, until a viscous syrup forms; to 56 parts of this syrup, add 44 parts of a mixture of equal amounts of lactic acid and liquid phenol, stirring often and well.

† Dr. C. P. Alexander, who prefers Canada balsam, pointed out that, in the Baltic Amber, he has 30 or 40 million years' proof that balsam is a good mounting medium!

Larvae and pupae.—If larvae are taken in the late third or fourth instar, they will need little attention when brought into the laboratory. Rearing dishes must become neither too warm nor too dry; and, while the minimum lethal temperature is not known for any species, larvae were lost in considerable numbers at times when the room in which they were kept became warmed to temperatures that are only comfortable to humans. It has been stated that larvae of *Dolichopeza* inhabit dry moss. It is, however, difficult to estimate the actual moisture content of such a habitat, and the fact is that the larvae were usually found unable to survive one night in a covered dish containing no apparent moisture.

Rearing larvae from eggs is a difficult task, and my attempts to do this have not met with notable success. However, the following methods have been found workable. Adult females in breeding cages (wide-mouth, half-gallon canning jars were found adequate) will oviposit on moist pads of paper (commercial cleansing tissues were used) and sometimes on the sides of the jar. At the end of the laying period, these pads may be removed and the eggs concentrated upon a circular portion of the paper, such as will fit into a Syracuse dish, or the like. Eggs left in the jar may be removed by washing them down with water (at room temperature) and collecting them in a pipette or dropper. Heavier than water, they will collect in the tip of the pipette and may be transferred to the moist paper pad without overly wetting it. When the eggs are about five days old, fragments of moss should be placed beneath the paper, and the larvae, upon hatching, will migrate to this moss. Excessive moisture in the dish is to be avoided, for the eggs will not mature if submerged, and the very young larvae drown readily in even small amounts of free water beneath the paper. No more water should be in the dish than will be retained by the paper, but the dish should be kept damp by the use of a cover and the occasional replacement of evaporated moisture. Larvae feeding under the paper may be observed through the bottom of the inverted dish, to which the pad will adhere by its dampness.

As the larvae grow larger, increasing amounts of moss should be placed in the dish, but separated leaves and stems should still be used, in order that the activities of the larvae may be watched at any time and head capsules or cast skins may be recovered after each molt. When larvae have at last transformed into the fourth instar, moss clumps in their natural form may be used, for the last larval skin may be recovered from the pupal burrow, and the larvae are large enough to be located and observed easily.

After formation of the pupa, it becomes necessary to move specimens to a larger dish, so that there will be sufficient space for emergence of the adult. Unlike some other tipuline pupae, those of *Dolichopeza* are not very active and will usually remain in any artificial "burrow" that is arranged in the moss for them. It is, of course, possible to bring larvae through all instars and pupation in a large dish, such as is recommended for pupae, but observation is very difficult and recovery of molted skins is practically impossible under such conditions.

In order to avoid overheating larvae and pupae during microscopic examination, I have used a device containing an ordinary 150-watt electric lamp, with a water-filled Florence flask in front of it, serving both to absorb heat and condense the light into a very intense spot. While larvae are seldom found feeding in the light in their natural surroundings, they rapidly accommodate to the increased illumination of the laboratory and may continue eating even while being observed in the bright light of the microscope lamp.

For studying preserved immature stages, I have used a Stender dish about one-third filled with paraffin, into which were carved such shapes and sizes of holes as were necessary to hold the specimens still, under alcohol.

It might be appropriate to say a few things about laboratory culture of mosses. To begin with, it is advisable to keep a covered terrarium stocked with food mosses at all times during the rearing period, and to take from such stock supplies whatever moss is needed to maintain adequate food in the rearing dishes. Isolated cushions of moss tend to become dehydrated and overgrown with molds. When larger quantities of moss are grown together, normal nutrient substrate may be retained and the mosses grow more luxuriantly, while molds seem less able to gain a foothold. Varying the depth of damp sand beneath the terrarium mosses provides a moisture gradient, and mosses may be placed according to their natural water requirements. Mosses which begin to mold should be removed from the terrarium. It has been observed that molds are less likely to occur if the terrarium is kept in a cool, though lighted situation.

ADULTS—EXTERNAL MORPHOLOGY

General description.—Smaller than most of the Tipulinae and larger than the average of genera of the Limoniinae, *Dolichopeza* is medium sized, as crane flies go. The body length from front of head to tip of abdomen varies from about 7 to 15 mm., depending upon the species. Except in one species, *Dolichopeza polita* (all its races), males average somewhat smaller in all dimensions than females. Wing length is approximately 8 to 15 mm. and again depends upon the species. Over-all size may vary not only with species but also with ecological fluctuations, as will later be explained in detail. Those characteristics which distinguish *Dolichopeza* from other tipuline genera have already been noted. The combined lengths of femur and tibia considerably exceed that of the wing, and the length of these two leg segments together is nearly always equalled or surpassed by that of the tarsus. The genus takes its name from this most striking feature; Greek *dolichos* = long, *peza* = foot. (*Oropeza* means "mountain-foot" and is derived from the Greek word *oros* = mountain.) This remarkable leg length, coupled with extreme slenderness, gives species of this genus a very characteristic appearance; it is what led one author to describe the legs of *Dolichopeza* as "excessively long."

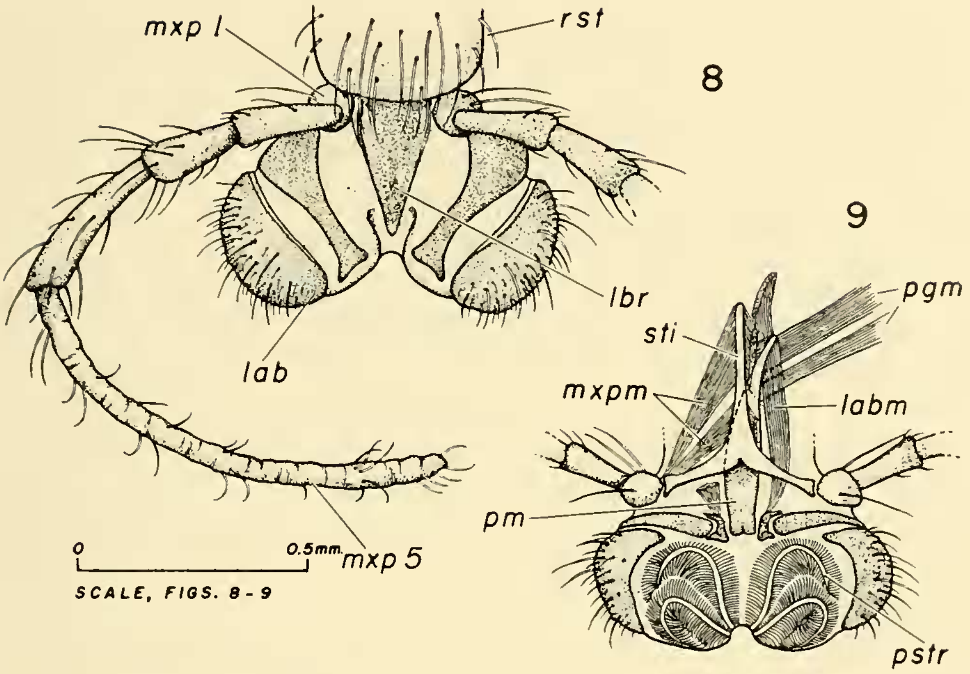
Head.—Most of the surface of the head is occupied by the large, dichoptic compound eyes, which are of about equal size in both sexes and of a black color. There are no ocelli, which is characteristic of all Tipulidae. Surface areas of the head capsule proper, such as the occiput, vertex, front and genae, are poorly defined, but the clypeus is distinct, forming the upper (anterior) and lateral parts of the rostrum, or proboscis. There is no nasus on the rostrum in the North American species.

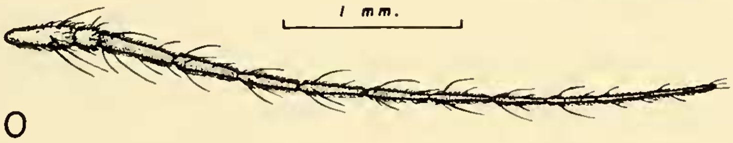
The antennae are composed of a rather cylindrical scape about four times as long as its width, a subspherical pedicel, and a flagellum of elongate, verticillate, more or less cylindrical segments, each somewhat thicker at the base than at the tip, and each beyond the first ordinarily shorter than the preceding segment (Fig. 10). In the subgenus *Dolichopeza*, there are ten flagellar segments (cf. Alexander, 1919:853), while in *Oropeza* there are eleven.

The rostrum bears the mouthparts, conspicuous among which are the two labellar lobes (apparently modified labial palps), each nearly covered on its oral surface by a system of pseudotracheae branching from two arcuate channels that convey liquid food to the tip of the hypopharynx, concealed beneath the heavily sclerotized, triangular labrum (Fig. 9). Peterson (1916:39) states that ". . . no piece is present at the base of any generalized palpus (of the Diptera) which can be homologized with the palpifer of generalized insects." He is supported in this opinion by Rees and Ferris (1939:146), Crampton (1942:34) and others. Accordingly, the basal portion of the maxillary palp (Fig. 8) is here interpreted not as a palpifer but as one of five segments, the terminal one of which is longer than all the others combined, as in all Tipulinae. The maxillary palp attaches to a sclerotized structure which, although it is mostly internal, is here considered to be the stipes of the maxilla, on the basis of musculature (Fig. 9). The structure I interpret to be formed of the partially fused stipites has been called the "apodeme of the cranial flexor muscle of the lacinia" by Rees and Ferris (1939) and the "maxillary apodeme" by Crampton (1942).

Thorax.—In either dorsal or lateral aspect (Figs. 14, 15), the external thoracic surface is dominated by the sclerites of the mesothorax, which contains the flight muscles. Seen from above, the pronotum (pn) is a narrow, convex band, almost concealed beneath the prescutum, while the mesothoracic postnotum completely obscures the metanotum. Several clearly defined areas comprise the mesonotum; these are the prescutum (psc), medially divided scutum (sc), scutellum (scl) with a parascutellum (pasc) on each side, and a postscutellum (pscl), or postnotum. The term "thoracic dorsum," used in descriptive paragraphs of this paper, refers to the mesonotum, which sometimes bears conspicuous color markings, especially on the prescutum. The broadly V-shaped, complete transverse suture between prescutum and scutum is characteristic of the entire family Tipulidae. On each anterolateral margin of the prescutum is a shallow indentation, the pseudosuture or pseudosutural fovea (psf).

All three pleural sutures are distinct and the sclerites of the pleural region easy to identify (Fig. 14). There is, however, some difference of opinion as to what these sclerites should be called. Between the pronotum and anterior coxa is the prothoracic episternum. Just forward of this is a cervical sclerite, and along its posterior side is the small epimeron of the prothorax. The corresponding parts of the metathorax, located between the third coxa and the base of the haltere, are somewhat less clearly outlined. Extending from the second coxa to the base of the wing is the conspicuous pleural suture of the mesothorax. Immediately anterior to this is the mesepisternum, divided, sometimes indistinctly, into a dorsal anepisternum and a ventral pre-episternum (called sternopleurite by Alexander, 1942:199), which adjoins the coxa. Spots of dark color are found on these two areas, in certain species. Between the second and third coxae and rather closely applied to the former is the meron of the mesothorax (episternum, in Alexander, 1942:199), sometimes darkly marked. Above this is an irregularly shaped mesepimeron, or pteropleurite, which is





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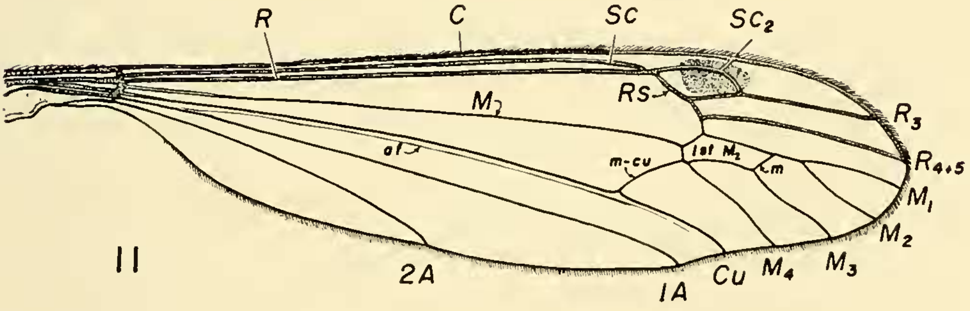
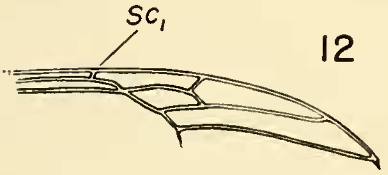




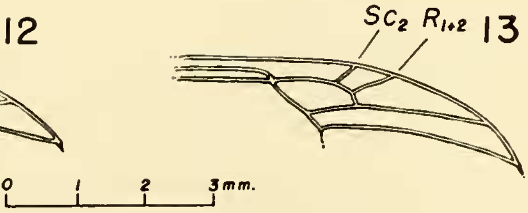


FIG. 8. Mouthparts of *Dolichopeza (Oropeza) polita*, antero-dorsal aspect; lab—labellar lobe, lbr—labrum, mxp 1—first segment of maxillary palp, mxp 5—fifth segment of maxillary palp, rst—rostrum. FIG. 9. Same as 8, postero-ventral aspect; labm—muscle of the labellar lobe (labial palp), mxpm—muscles of the maxillary palp, pgm—muscles originating on postgena and inserting on prementum, pm—prementum, pstr—pseudotrachea, sti—partially fused stipites. FIG. 10. Antenna of *Dolichopeza (Oropeza)* sp. FIG. 11. Wing of *Dolichopeza (Oropeza) carolus;* A—anal veins, af—anal fold, C—costa, Cu—cubitus, M—media, m—medial cross-vein, m-cu—median-cubital cross-vein, R—radius, Rs—radial sector, Sc—subcosta. FIG. 12. Wing of *Dolichopeza (Oropeza) carolus* showing the vein Sc_1 present. FIG. 13. Same as 12, showing the vein R_{1+2} present.

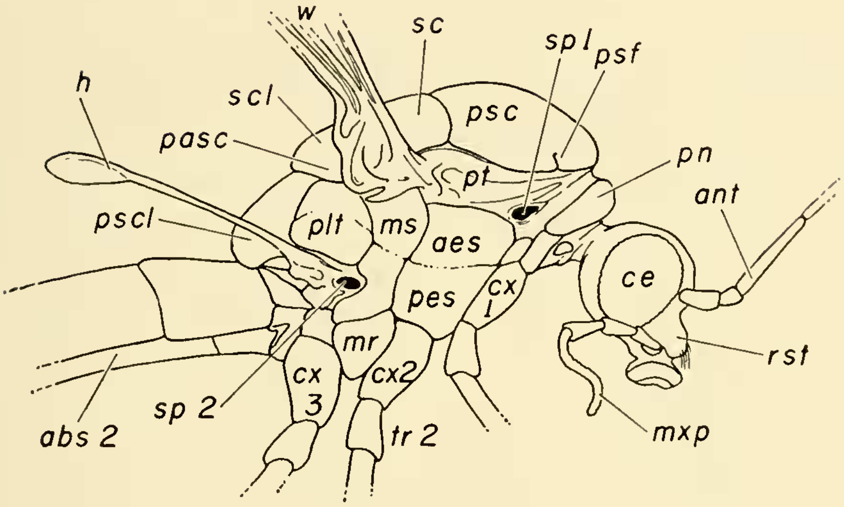
weakly divided into an anepimeron and katepimeron and is ordinarily unicolorous. Between the mesepimeron and the postscutellum lies a sclerite known as the pleurotergite, which Crampton (1942:49) states is actually a lateral division of the postscutellum. What I have called the postscutellum is referred to as the mediotergite of the postscutellum by Crampton.

The mesothoracic spiracle is situated in a membranous area at the anterior edge of the segment, between the anepisternum and prescutum, and the metathoracic spiracle lies just in front of the base of the haltere.

All species of *Dolichopeza* in North America have the wings unmarked except for narrow tinged bands along certain veins (especially the cubitus and m-cu cross-vein) and a weakly or strongly colored, brownish stigmal spot. Figure 11 illustrates the typical venation of subgenus *Oropeza*, in which the costa, subcosta and radius, including all its branches, are considerably heavier veins than any others. The humeral cross-vein is present, and the arculus is complete. Occasionally the vein Sc_1 is found in the position indicated in Figure 12, and rarely R_{1+2} is present (Fig. 13). Spurious cross-veins have occasionally been observed, especially between veins R_3 and R_{4+5}. As mentioned earlier, the cell 1st M_2 (discal cell) does not occur in the subgenus *Dolichopeza* (compare Figs. 1, 2). Designation of all veins follows the system used by Alexander (1942: 201).

Both the femora and tibiae are of a length about equal to that of the fly's abdomen, and the first segment of the tarsus alone is often longer than these two together. Each tarsal segment is of greater length than all those beyond it combined. The tibial spurs are slender and inconspicuous; they arise perpendicular to the axis of the tibia but bend sharply, so that the tip is nearly parallel to the tibia. The shape of these spurs seems to be the same in all species. Likewise, there is no apparent difference, from species to species, in the untoothed tarsal claws. Leg coloration aids in species identification, although any species may be properly identified by the use of other characters.

Male abdomen.—There are nine evident segments of the male abdomen (Fig. 16), the last of which, called the hypopygium, bears the genital appendages and other reproductive structures. The first and second terga are more or less fused, and the first sternum is shorter than the corresponding tergum. The third through eighth segments are unmodified. The tenth or anal segment (as) is represented by a membranous projection surrounding the end of the



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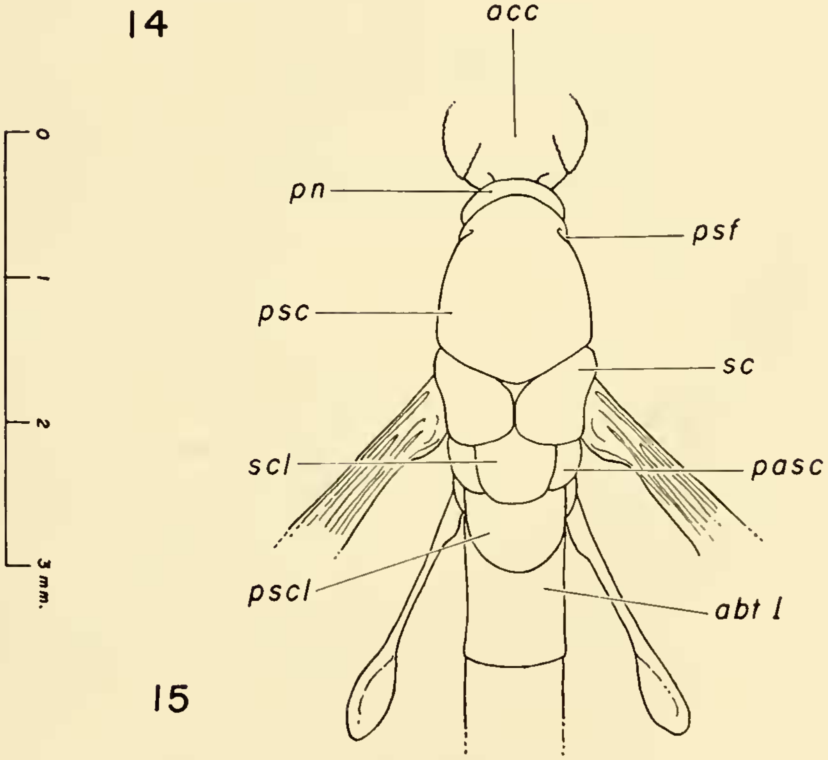

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Fig. 14. *Dolichopeza (Oropeza)* sp., right lateral aspect of thorax; abs—abdominal sternum, aes—anepisternum, ant—antenna, ce—compound eye, cx—coxa, h—haltere, mr—meron of mesothorax, ms—mesepimeron, mxp—maxillary palp, pasc—parascutellum, pes—pre-episternum of mesothorax, plt—pleurotergite, pn—pronotum, psc—prescutum, pscl—postscutellum, psf—pseudosutural fovea, pt—paratergite, rst—rostrum, scl—scutellum, sc—scutum, sp—spiracle, tr—trochanter, w—wing. Fig. 15. Same as 14, dorsal aspect; abt—abdominal tergum, occ—occiput, other abbreviations as in 14.

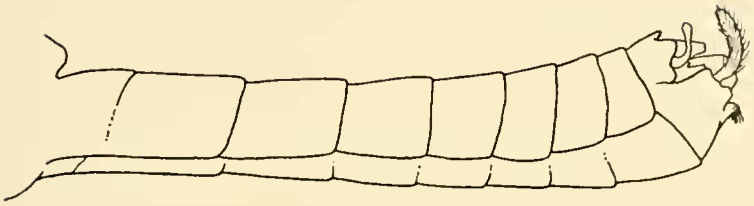
digestive tube and situated close beneath the middle of the ninth tergum.

It seems probable that in primitive Diptera there were paired genital appendages, each comprising a basal and a distal segment, arising from the ninth abdominal segment in somewhat the arrangement found in existing Mecoptera—*Panorpa,* for example. These appendages appear to be highly developed lateral phallic lobes (Snodgrass, 1957: 44-47), although they have been widely regarded as modified abdominal limbs, or gonopods. In the Tipulinae, the basal portion (basimere, or coxite, of morphologists), which has been called the basistyle (Fig. 18, bs), is completely fused with the ninth sernum (s9). The distal portion (telomere, or stylus) in many crane flies has become divided into two separately articulated appendages (Fig. 17), a dorsal or outer dististyle (od) and a ventral or inner dististyle (id). The shapes of these structures can be used to a limited extent in classification.

The ninth tergum in the subgenus *Oropeza* bears heavily sclerotized lateral extensions, which may be called tergal arms (ta) and which function to brace the ventral valves of the female ovipositor during copulation. These have characteristic shapes, depending upon the species. While no such structures are found in the subgenus *Dolichopeza,* their absence is compensated by other parts of the hypopygium. I have been unable to learn any function of the various forms of the posterior margin of the ninth tergum, but it is a fortunate coincidence that this sclerite offers one of the most reliable means for species determination in males. It may be shallowly or deeply emarginate or crenulate, or may bear a median projection with sharp teeth or blunt lobes.

Between the basistyles, on either side of the midline of the ninth sternum, are the gonapophyses (gon), the various shapes of which have already been briefly discussed. The term "gonapophyses" has been used in many ways in the several orders of insects, but most authors agree that the gonapophyses of male insects are median projections in proximity to the gonopore. The origin and homology of the gonapophyses in *Dolichopeza* are unknown; Figure 29, however, indicates the close relationship between them and the adminiculum and basistyles. It seems advisable to retain the term for these particular structures since it does not appear to be misapplied.

The male intromittent organ, or penis (Fig. 17, p) is an extensible, slender and rather densely sclerotized tube, straight tipped, or nearly so, in some species and abruptly curved at the tip in others.



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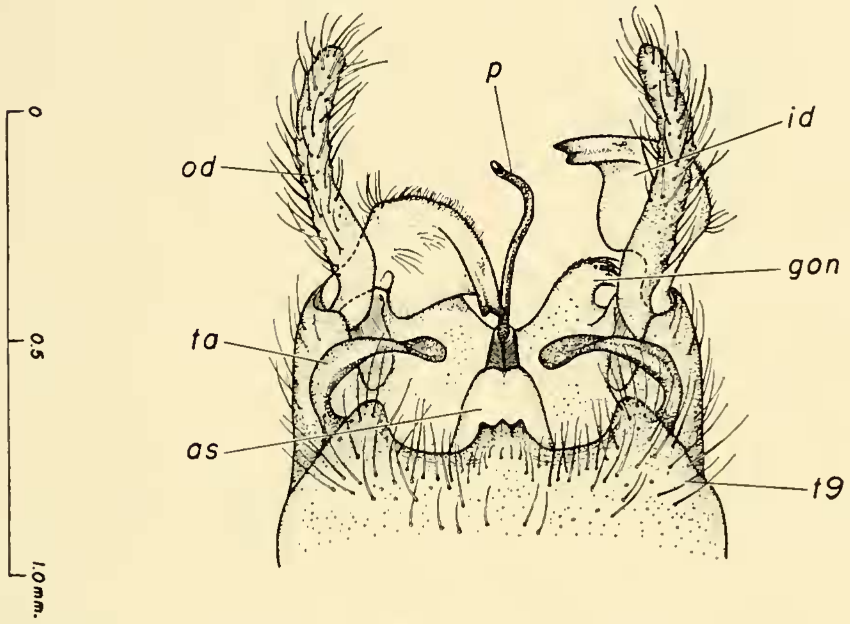

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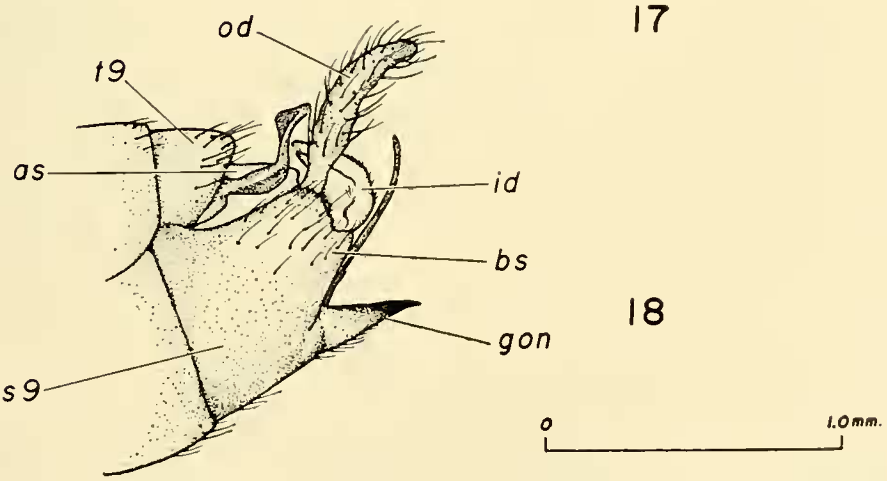

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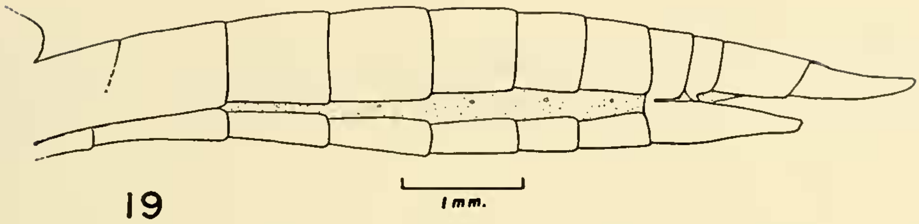
FIG. 16. Abdomen of male *Dolichopeza (Oropeza) tridenticulata*, left lateral aspect. FIG. 17. Hypopygium of male *Dolichopeza (Oropeza) tridenticulata*, dorsal aspect; as—anal (tenth) segment, gon—gonapophysis, id—inner dististyle, od—outer dististyle, p—penis, ta—tergal arm (lateral arm of ninth tergum), t9—ninth tergum. FIG. 18. Hypopygium of male *Dolichopeza (Oropeza) venosa*, left lateral aspect; bs—basistyle, s9—ninth sternum, other abbreviations as in 17.

Its method of extension will be explained later. Where the penis emerges from the floor of the genital chamber, it is braced by a cone-shaped, intensely sclerotized structure (Figs. 17, 28) that is actually formed from partial or complete fusion of two elements, one on either side. This has been termed the aedeagus by Alexander (1942, etc.) and the adminiculum by Mannheims (1951:10), Snodgrass (1957:45) and others. Its two component parts have been regarded as parameres (Tjeder, 1948), hypomeres (Rees and Ferris, 1939) and mesomeres (Snodgrass, 1957). These parts extend cephalad in the floor of the genital chamber and enter the abdominal cavity as short apodemes supporting the vesica (Figs. 28, 29). The term "aedeagus" has been used synonymously with what I have designated as the penis, also for the penis and its basal structures combined, and in other more restricted senses, almost always, however, as a phallic structure. Accordingly, I have adopted the term "adminiculum," meaning a support, for the function of this cone-shaped structure in *Dolichopeza* is strictly one of support and not intromission in any way.

Female abdomen.—There are ten clearly defined segments in the female abdomen, of which the eighth through tenth are modified to form the ovipositor (Fig. 19). As in the male, the first and second terga are somewhat fused, and the first sternum is shorter than the corresponding tergum. The third through seventh segments are unmodified. Small spiracles occur in the membranous pleura of the first seven segments but are usually concealed by overlap of the sclerites if most of the eggs have been laid. Except for the first, which has shifted to the forward edge of its segment, the spiracles are all near the midlength of their respective segments.

It has been argued by Crampton (1942:81) that the type of egg laying apparatus found in *Dolichopeza* and other crane flies ". . . should be referred to as an oviscapt, or ovicauda, rather than an 'ovipositor' . . . since its parts are not strictly homologous with those of a true ovipositor of the type occurring in orthopteroid insects." However, as the structure takes its name from its undeniable function of oviposition rather than from any homology, the term "ovipositor" is retained. In the typical pterygote ovipositor, the gonopore, opening between the eighth and ninth sterna, is flanked by a pair of blade-like valvulae, attached to basal sclerites (first valvifers) belonging to the eighth sternum, and two pairs of similar valvulae belonging to the ninth sternum. The latter pairs are attached to common bases (second valvifers) at either side, and



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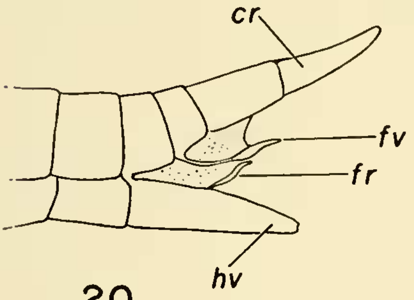

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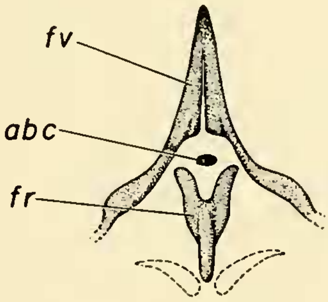

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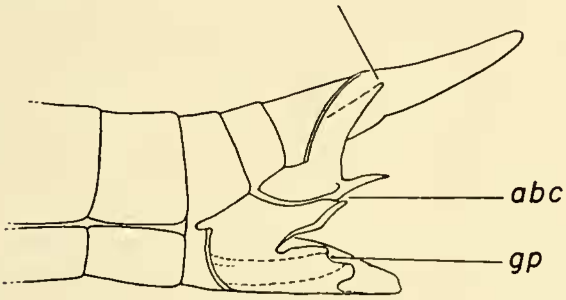

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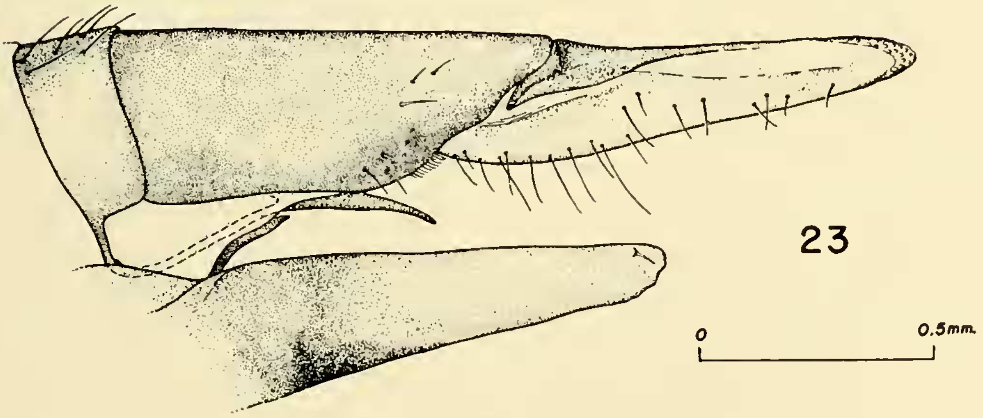

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FIG. 19. Abdomen of female *Dolichopeza (Oropeza) tridenticulata*, left lateral aspect. FIG. 20. Same as 19, showing details of ovipositor; cr—cercus, fr—furca, fv—fused valvulae (ninth sternum), hv—hypovalve (extended eighth sternum). FIG. 21. Details of external reproductive structures of female *Dolichopeza (Oropeza) similis*, postero-ventral aspect; abc—aperture of bursa copulatrix, other abbreviations as in 20. FIG. 22. Details of reproductive structures of female *Dolichopeza (Oropeza) tridenticulata*, left lateral aspect, cut-away view; a—anus, abc—aperture of bursa copulatrix, gp—gonopore. FIG. 23. Ovipositor of female *Dolichopeza (Oropeza) johnsonella*, left lateral aspect, showing sensory structures.

all together comprise the ninth sternum. Snodgrass (1935:611) says of these, "The second valvifers usually retain a close connection with the tergum of the ninth segment, but the first valvifers are often more or less dissociated from the eighth segment." Above and to the rear of the typical ovipositor are the tenth and eleventh abdominal segments, with cerci arising from the membrane between them and with the anal opening situated close beneath the eleventh tergum.

The structure found in females of *Dolichopeza,* as in other tipulids, does not depart from this basic arrangement of parts except in details. Completely encircling the eighth abdominal segment at its anterior end is a rather strongly sclerotized ring which narrowly connects the tergum and sternum (Fig. 20). While the tergum is otherwise unmodified, the sternum is projected backward to beneath the tenth tergum, or further, in the form of a pair of egg guides, or hypovalves (hv), which however are fused nearly to their tips in the genus *Dolichopeza.* These hypovalves are pocketed on their inner surfaces to receive the tips of the inner dististyles of the male, in order to effect a firm attachment in copulation. Rising slightly from the inner floor of the hypovalves is the membranous end of the median or common oviduct, terminating in the gonopore (Fig. 22, gp). There is, in the narrow ninth segment, a modification of the sclerotized anterior ring found in the eighth. Semicircular above, where it corresponds to the anterior margin of the tergum, this band is, at the sides, deflected abruptly caudad and toward the midline, where its ends meet to form a fairly heavily sclerotized, triangular blade, which may be regarded as the fused second valvulae (Figs. 20, 21, fv), and thus the ninth sternum. Snodgrass (1903: 178) has called these the fused second gonapophyses. Between this reduced ninth sternum and the hypovalves, or eighth sternum, is the genital chamber. Immediately below the ninth sternum is the upper opening of the reproductive system, that which leads into what may be called the bursa copulatrix, since it is into this opening that the penis of the male is inserted in mating (Figs. 21, 22, abc). Thus, while it would seem that the two separate parts of the reproductive system open independently to the outside, it may be seen that both in fact enter the genital chamber as above defined.

Lying in the membrane beneath the aperture of the bursa copulatrix is a sclerotized fork, of which one tine extends to either side of the aperture. The base of this fork is in a pouch formed just above the oviduct (Fig. 22), and it sometimes happens that the floor of this pouch (that is, the roof of the oviduct) bears small, usually weakly sclerotized areas, closely associated with the base of the fork, as indicated by the broken lines in Figure 21. Students of the Psychodidae (especially *Phlebotomus*) have called this fork the furca, the name that is adopted here (Figs. 20, 21, fr). Snodgrass (1903: 178) is of the opinion that the furca ". . . may be the fused and rudimentary anterior gonapophyses," by which he means the first valvulae and their valvifers in the sense used above.* This seems a sound interpretation in spite of the great modification of the parts involved.

The tenth segment has a saddle-like and strongly sclerotized tergum (Fig. 23) but no sclerotized sternum. Beneath the posterior end of the tenth tergum is situated the anal opening. As in most crane flies, the cerci are strongly sclerotized and blade-like in shape, reinforced along their dorsal edges. Minute pegs grouped at the tips of the cerci (Fig. 23) are thought to be sensory in function, and it sometimes seems that females in the process of oviposition obtain impressions about the nature of the substrate by means of probing with the cerci. Inasmuch as the cerci have an important function also in the actual deposition of the eggs, they may be termed the dorsal (or "tergal") valves of the ovipositor. A small, indistinct sclerite between the bases of the cerci may be interpreted as the eleventh tergum.

ADULTS—INTERNAL MORPHOLOGY

Head.—Much of the interior of the head is occupied by portions of the central nervous system, particularly the brain and the large optic lobes, the convex apical surfaces of which are in contact with the basement membranes of the compound eyes. The only other conspicuous structures are the anterior parts of the digestive tube (Fig. 26). In the rostrum, the epipharynx (eph) and hypopharynx (hph) are fused basally, forming a partly sclerotized tube, the basipharynx (bph), which can be dilated by means of a thick muscle attached to its roof and originating on the anterior wall of the rostrum, or clypeus. Flexibly joined to the upper end of the basipharynx is the pharyngeal pump, a structure made up of three sclerotized elements connected by elastic membranes to form a tube that is somewhat expanded at each end and roughly triangular in cross section. Some authors have applied the term oesophageal pump to the pharyngeal pump. The arrangement of attached muscles suggests that dilation of the aboral end of the pharyngeal

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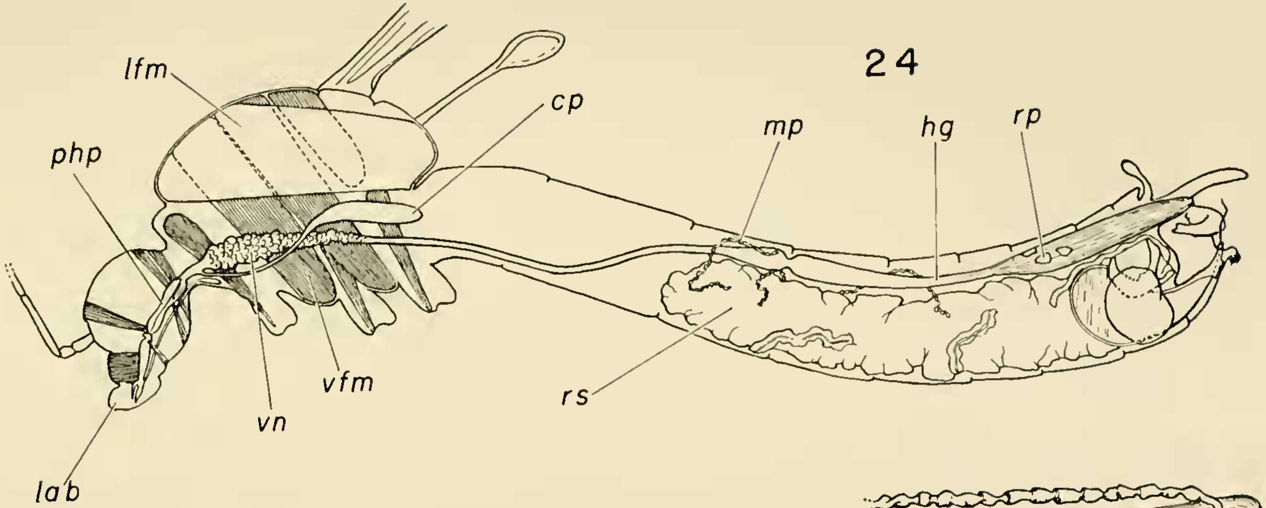
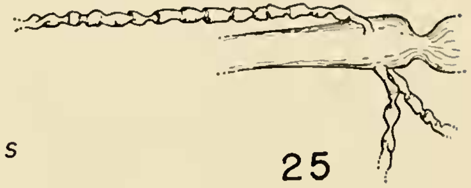
* It is inadvertently stated by van Emden and Hennig (1956: 121) that Snodgrass homologized the hypovalves with the anterior gonapophyses.





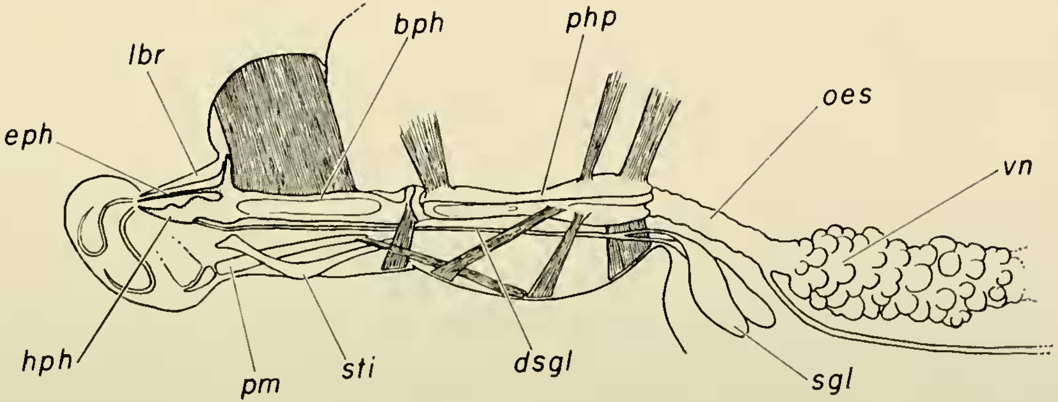


FIG. 24. Gross internal anatomy of adult male *Dolichopeza (Oropeza) tridenticulata;* cp—crop, hg—hind-gut, lab—labellar lobe, lfm—longitudinal flight muscle mass (shown as unshaded area superimposed over shaded vertical flight muscles), mp—Malpighian tubule, php—pharyngeal pump, rp—rectal papilla, rs—reproductive structures (shown as compact, intertwined mass heavily invested with adipose tissue), vfm—vertical flight muscles, vn—ventriculus. FIG. 25. Detail of digestive system of *Dolichopeza (Oropeza)* sp., showing appearance of Malpighian tubules in preserved specimen. FIG. 26. Details of digestive system, anterior portion; bph—basipharynx, dsgl—common duct of salivary glands, eph—epipharynx, hph—hypopharynx, lbr—labrum, oes—oesophagus, php—pharyngeal pump, pm—prementum, sgl—salivary glands, sti—stipes of maxilla, vn—ventriculus.

pump provides most of its action. A single salivary duct leads from the ventral side of the hypopharynx along the pharynx to the neck region, where the duct divides into two (Fig. 26). There is no tentorium.

Thorax.—By far the greatest volume of the thoracic cavity is taken up by the flight muscles: lateral, vertical bands and two large, longitudinal muscle masses, one on either side of the median plane, as outlined in Figure 24. A short length of membranous esophagus connects the oesophageal pump with the ventriculus in the cervical region. There appears to be no proventriculus. The anterior end of the ventriculus has a decidedly lumpy surface, the nodules being largest just behind the neck and diminishing in size until inconspicuous about midway through the thorax. A membranous crop, which with its duct-like proximal portion extends nearly the full length of the thorax, is attached ventrally at the junction of the oesophagus with the ventriculus (Fig. 26). Just within the thorax, beneath the oesophagus, lie the two small salivary glands, the ducts of which unite quite abruptly. The ventral nerve cord, passing through the thorax from the suboesophageal ganglion, produces three large thoracic ganglia, close below the digestive tube. These give off branches to the thoracic appendages and muscles.

Abdomen.—Except for varying amounts of fat tissue and the thin bands of muscles in the body wall, the contents of the abdomen consist almost entirely of the reproductive system and parts of the slender alimentary canal. Pale greenish gray and shining in a freshly killed fly, the reticulated fat tissue, most abundant in males, is dull white in specimens preserved in alcohol. The ventriculus, entering the abdomen along the floor of the first segment, curves up against the body wall to terminate dorsally in the third abdominal segment, at the point where the four Malpighian tubules attach. These excretory outgrowths are about as long as the entire body and are either coiled mostly in the upper part of the abdominal cavity or are intertwined among the other organs. In life, their color is mottled gray, but alcohol preservation usually renders them pale brown or reddish brown; also in life there may be a zone of yellowish coloration about the attachment of the Malpighian tubules. The hindgut is slightly enlarged at its anterior end, tapering evenly to the rectum, a thin walled and sac-like structure close beneath the seventh, eighth and ninth terga. Four irregularly oblong rectal pads (Snodgrass, 1935: 381) of opaque white color lie in the anterior part of the membranous rectal wall.

Male reproductive system.—A conspicuous arrangement of strongly sclerotized parts, lying primarily in the eighth and ninth abdominal segments, is visible in specimens cleared in KOH for mounting on microscope slides. These structures have been studied, variously named and employed in classification by many investigators (Snodgrass, 1904; Tokunaga, 1930; Edwards, 1938; Tjeder, 1948; Mannheims, 1951; Wood, 1952). As described earlier, each of the two elements forming the conical adminiculum is continuous with a flattened, sclerotized rod lying in the membranous floor of the genital chamber. Upon the anterior tips of these rods, which project into the abdominal cavity as apodemes, rests a bulb or capsule, which is joined to the base of the penis (Fig. 28). This has been called the spermatophore sac by Tokunaga, and the central vesicle by Snodgrass. Following the terminology used by Edwards (1938: 14), it is here called the vesica. As the vesica is capable of rotation in the sagittal plane, rocking on the tips of the adminicular rods, it is difficult to describe its parts as being dorsal or ventral, anterior or posterior, as can be done for those genera in which this organ is fixed in position. However when the penis is fully retracted, the vesica has the position indicated in Figure 28, and the following description is based upon the structure thus oriented. There are two wing-like outgrowths from the anterior surface of the vesica, one arising at either side of the base of the penis and curving down along the side of the bulb to about the point of flexible attachment of the vesica to the adminicular rods. These are the lateral apodemes (lap). From the posteroventral surface of the vesica extend two rather stout rods, diverging backward, which I have called the posterior apodemes (pap). A transverse, fan-shaped and nearly semicircular apodeme arises from the posterodorsal surface of the vesica; this is the dorsal apodeme (dap). It has a thickened median keel at the base of which is an almost hemispherical, heel-like piston that compresses the vesica when muscles between the dorsal and lateral apodemes are contracted. Muscles between the dorsal and posterior apodemes serve to dilate the vesica. From the vesica, the penis curves forward and downward, within a membranous pouch, through the seventh segment to the floor of the eighth and so out through the adminiculum. The membranous pouch could be regarded as a narrow but deep continuation of the genital chamber, as it is open to the outside at the adminiculum.* The membrane is suspended at either side from the adminicular rods, the anterior end of the pouch being closed

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* In some species of *Tipula* I have examined, the opening continues cephalad between what appear to be equivalents of the adminicular rods.

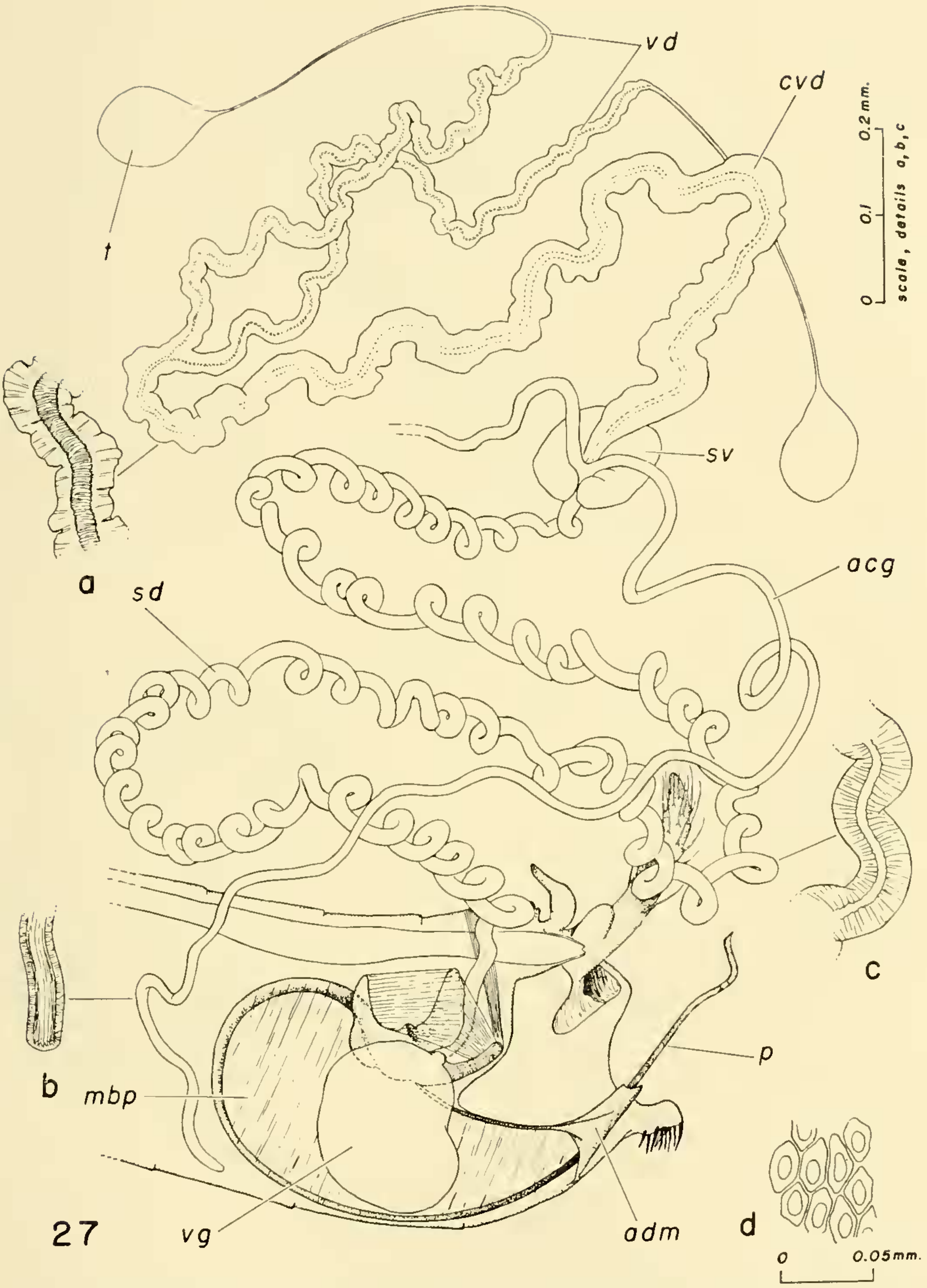


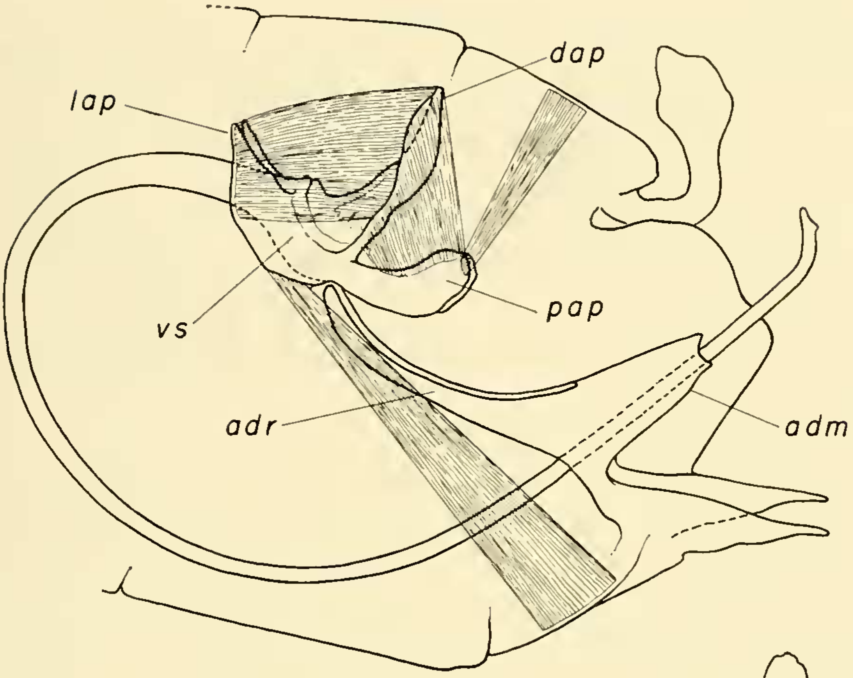
Fig. 27. Details of reproductive system of male *Dolichopeza (Oropeza) polita* ssp.; acg—accessory gland, adm—adminiculum, cvd—common vas deferens, mbp—membranous pouch enclosing penis, p—penis, sd—seminal duct, sv—seminal vesicle, t—testis, vd—vasa deferentia, vg—vesicular gland. Enlarged insets: a—common vas deferens, b—accessory gland, c—seminal duct, d—vesicular gland.

beneath the vesica and around the base of the penis. Contraction of muscles originating on the ninth sternum and inserting on the anterior faces of the lateral apodemes brings about rotation of the vesica and exsertion of the penis, which action is aided by small muscles connecting the posterior apodemes with the ninth tergum.

The nonsclerotized parts of the male reproductive system are usually complexly intertwined and difficult to disentangle. They have rarely been examined in detail in any Tipulidae (see Keuchenius, 1913) and, so far as I am aware, never in the genus *Dolichopeza.* I have unraveled this mass of tubes in most species of North American *Dolichopeza* and have found a rather consistent pattern, illustrated by the example of *Dolichopeza* (*Oropeza*) *polita* ssp., in Figure 27. There are two thin walled, bladder-like testes (t), which usually lie one before the other near the anterior end of the mass of the reproductive system. In a freshly-killed fly, these are usually found full of spermatozoa. The testes empty into the vasa deferentia (vd), which are at first exceedingly slender, then thick-walled and finally merged into a common vas deferens (cvd) with thick, irregular, possibly glandular walls enclosing a more or less central tube (Fig. 27a). The vasa deferentia are hyaline in appearance and are easily recognized among the abdominal contents by their glossy sheen.

The common vas deferens terminates in the center of an enlarged, ring-shaped, glandular-walled seminal vesicle (sv). That this structure, and not the enlarged parts of the vasa deferentia (cf. Snodgrass, 1935: 568), is actually the seminal vesicle is indicated by its comparatively large lumen, in which masses of spermatozoa have been observed. Two elongate "accessory glands" (acg) also converge and join at the seminal vesicle. These tubular glands are of a diameter about equal to that of the Malpighian tubules, with a relatively large lumen and walls of apparently columnar cells (Fig. 27b). Their color in life is pale rusty, with a granular appearance, but preserved in alcohol they are a dull white. The connection of the seminal vesicle to the other organs is not easily traced; however, it appears that it joins them at one end only, the other end being looped around the bases of the vas deferens and the accessory glands until it touches the end with the opening.

From the confluence of all these organs, a long and much-coiled conduit leads to the posterior side of the vesica, between the posterior apodemes. This has been called the ejaculatory duct (Keuchenius, 1913, for *Tipula* sp.), but because I believe that term hardly describes its function, I have called it simply the seminal



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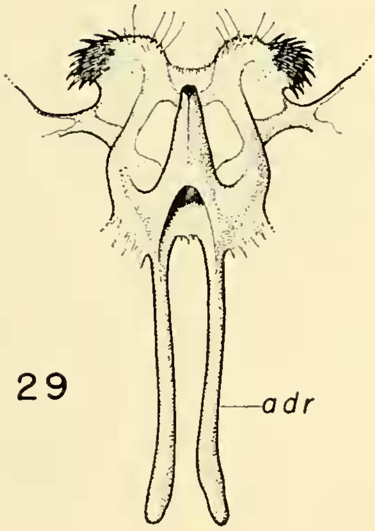

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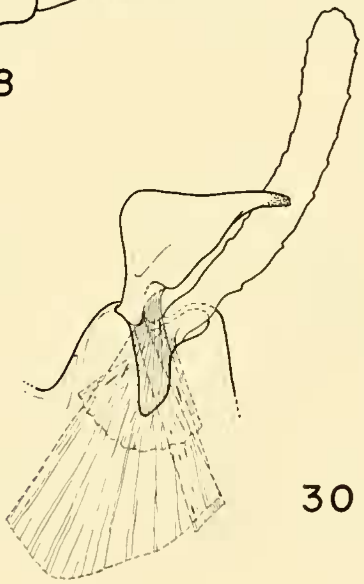

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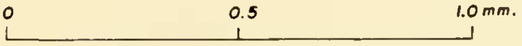


FIG. 28. Reproductive structures of male *Dolichopeza (Oropeza venosa;* adm—adminiculum, adr—adminicular rods, dap—dorsal apodeme, (compressor apodeme) of vesica, lap—lateral apodeme, pap—posterior apodeme, vs—vesica. FIG. 29. Reproductive structures of male *Dolichopeza (Oropeza) polita* ssp., dorsal aspect, showing relationship of adminiculum, adminicular rods and gonapophyses; adr—adminicular rod. FIG. 30. Left basistyle and dististyles of male *Dolichopeza (Oropeza) walleyi*, inner or mesial aspect, showing musculature (cf. Fig. 17).

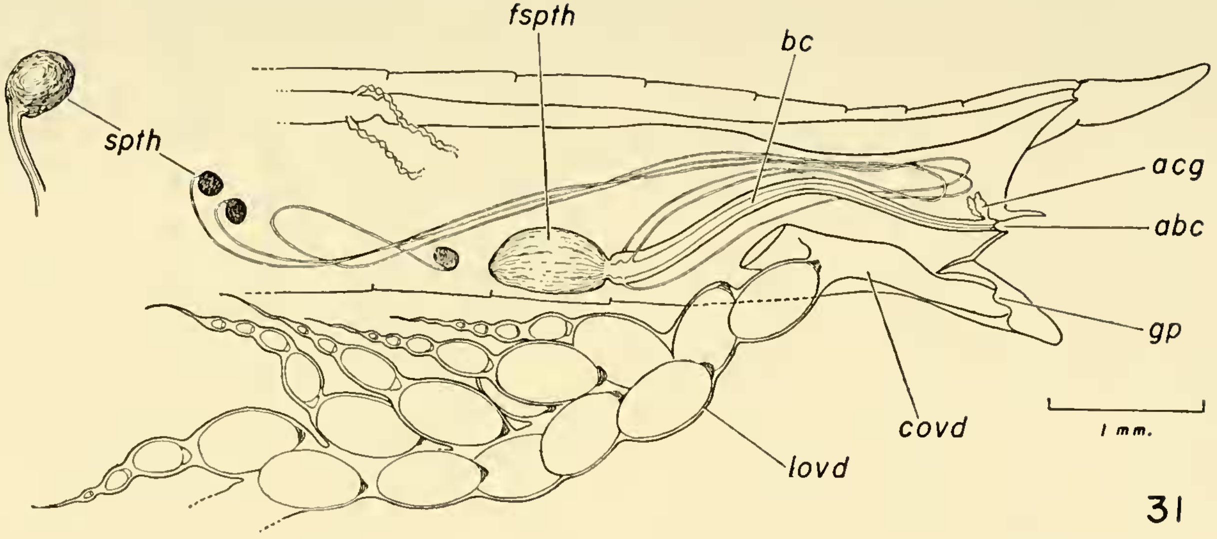
duct (sd). In species of the *obscura* group, the seminal duct is quite lengthy and is coiled in the manner of a spring, although the direction of coil is sometimes here and there reversed. Laid out more or less straight but with the small coils still in place, the seminal duct in a male *Dolichopeza* (*O.*) *polita* ssp. measured 23 mm. In *D. americana* and the *sayi* group, this duct is shorter and less tightly coiled, as a rule. In *D.* (*O.*) *carolus*, it is only about one-fourth to one-third as long as in *polita* but equally coiled and of about the same diameter as in the latter species. In *carolus* also the basal parts of the accessory glands are widened, rather resembling the common vas deferens.

Over-all length of the reproductive system from the vesica to the testis is about 45 mm., in larger species of the *obscura* group. From the seminal vesicle to the testis was 21.2 mm. in *obscura;* the common vas deferens measured 11.5 mm. in *polita.* In *americana* and the *sayi* group, the total length is about half as great, the difference in length of the seminal duct accounting for most of the decrease.

Perhaps most conspicuous among the nonsclerotized male reproductive organs are a pair of large, flattened, broadly reniform glands lying one at each side and somewhat below the vesica. Earlier authors seem not to have noticed these, but I have seen similar glands in *Tipula* spp. and other crane flies. They seem to reach their greatest development in *Dolichopeza.* The outer walls of these are smooth, but the inner surfaces have a vertically corded appearance and are made up of large, irregularly polygonal cells with large nuclei (Fig. 27d). The glands possess a lumen of capacity at least equalling that of the seminal vesicle and empty by ducts on their upper medial surfaces directly into the vesica. Judging from their size, they must contribute very significantly to the seminal fluid. The designation vesicular glands (vg) seems appropriate for these.

Female reproductive system.—The reproductive apparatus of the female *Dolichopeza* is divided into two portions: the bursa copulatrix and its associated structures, and the oviducts and their ovarioles. These two parts have separate external apertures, as discussed earlier under the external morphology of the females, and they seem to have no internal connections.

Leading cephalad from the gonopore is a thin-walled but muscular common oviduct (Fig. 31, covd), which in about the middle of the seventh abdominal segment divides into two lateral oviducts (lovd). These organs, because of their membranous structure, are



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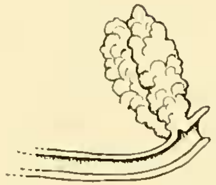

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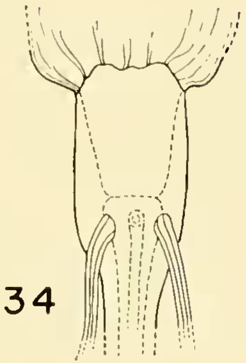

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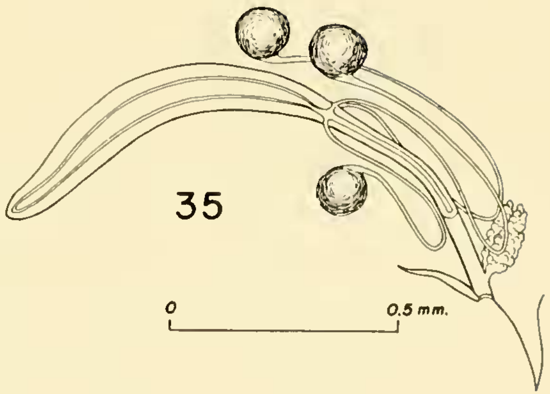

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Fig. 31. Internal reproductive structures of female *Dolichopeza (Oropeza) tridenticulata;* abc—aperture of bursa copulatrix, acg—accessory glands, bc—bursa copulatrix, covd—common oviduct, fspth—functional spermatheca, gp—gonopore, lovd—lateral oviduct, spth—spermatheca. Fig. 32. Two spermathecae of *Dolichopeza (Oropeza) carolus.* Fig. 33. Same as 31; detail of accessory glands. Fig. 34. Same as 31; anterior end of bursa copulatrix, dorsal aspect, showing attachment of spermathecal ducts. Fig. 35. Internal reproductive structures of female *Dolichopeza (Dolichopeza) americana.*

most easily seen in older females that have laid practically all their eggs. From each lateral oviduct, lying along the floor of the abdomen, the many ovarioles rise dorsally and bend anteriorly, their filiform tips often attaching to the dorsal or lateral abdominal walls. Within the ovarioles, eggs in increasing stages of development may be seen, from scarcely discernible specks in the upper ends to well formed but still pale colored eggs toward the lateral oviducts. In a newly-emerged female, the lateral oviducts and lowermost portions of the ovarioles are stretched taut with fully formed eggs, in which the chorion is already black and the terminal filaments (in those species that have them) completely developed. The eggs lie with their posterior ends directed toward the gonopore, which is also the way they are oriented in the ovarioles. In gravid females, eggs are found as far forward as the first abdominal segment, compressing the viscera tightly against the body wall.

In copulation, the penis of the male is inserted into the bursa copulatrix (bc), and the spermatozoa are presumably stored in the three spermathecae until the time of oviposition. The spermathecae (spth) are very small, intensely sclerotized capsules that are the only structures besides eggs to show at all clearly in flies that have been treated with KOH for mounting on microscope slides. They connect to the anterior end of the bursa copulatrix by filamentous ducts, two of which join the bursa dorsolaterally and one ventrally (Fig. 34). Their shape is nearly spherical in most species but flattened on the side of attachment in *Dolichopeza carolus* (Fig. 32). The spermathecal ducts are of great length and are thrown into long loops within the abdomen. In teneral females, the distal ends of these ducts, that is, the ends nearest the spermathecae, are soft, wrinkled and coiled. In older females, however, the ducts grow firmer, straighten out, and elongate, as the spermathecae move from the anterior end of the abdomen toward the middle or posterior regions. In *Dolichopeza americana*, the spermathecal ducts are shorter, and the spermathecae are usually found near the caudal end of the abdomen in both teneral and older flies (Fig. 35).

In species of the subgenus *Oropeza*, the bursa copulatrix extends cephalad to the sixth or fifth abdominal segment, while in *Dolichopeza* s. s. it is much shorter, scarcely half a millimeter in length (compare Figs. 31 and 35). The bursa has a thin, yellowish lining and a thick, whitish-transparent outer wall. A pair of nodular, whitish accessory glands (acg), the function of which in these flies is unknown, open into the bursa copulatrix on its dorsal wall near the aperture (Fig. 33).

A relatively large pouch joins the anterior end of the bursa copulatrix, only a short distance from the attachment of the spermathecal ducts. It is rather oval in shape, with thin wrinkled walls in species of the *obscura* group (Fig. 31), thicker-walled and more elongate in the *sayi* group, and rigidly thick-walled, elongate and curved in *Dolichopeza americana* (Fig. 35). Its connection to the bursa is somewhat different from species to species in *Oropeza*, as will be seen on comparison of Figures 31 and 34. Unable to find any structure in any other insect that is homologous with this pouch, and noting the wide opening from the pouch into the bursa copulatrix, I am inclined to regard the pouch as the functional spermatheca (fspth) and to suspect that the three small spermathecae are generally nonfunctional in *Dolichopeza,* and perhaps in other Tipulinae. This supposition finds some support in the fact that oviposition takes place very soon after mating and that the eggs are fertilized at the time of deposition, presumably by a flow of seminal fluid over them sufficient to insure that some spermatozoa will reach the micropyle of each egg; hence the supply of spermatozoa is presumably large and situated rather near to the opening of the oviduct. The spermathecae, on the other hand, are quite small, and their ducts are in some species nearly twice the length of the entire abdomen. It may be, of course, that the large pouch stores sperm for rather immediate use, while the spermathecae are reservoirs for several hours' on days' storage.

INTRASPECIFIC VARIATION

After studying many individuals of a species, it is possible to conclude, somewhat reliably, what is the normal or usual condition of practically any observable feature of the organism involved. On this basis, it is possible also to visualize an average individual of the species, in which means of dimension, color, shape and so on are combined. Then, all specimens at hand will be seen to deviate, in one way or another and to varying degrees, from the average. Small departures of common occurrence may, I believe, be regarded as falling within a normal range, while extraordinary individuals may be considered abnormal. It is also found, from time to time, that with respect to one or more characteristics individuals may group around two or more distinct means, in which cases special interpretation is required, for clines or geographic races may be indicated.

Some of the individual, intraspecific variation in *Dolichopeza* has been misinterpreted, as it has also in many other groups of organisms. It therefore has seemed worthwhile to attempt to classify the kinds of variation encountered and to indicate their probable causes. The classification that follows is not intended to be general in scope but applies only to variation observed in *Dolichopeza*. The kinds of variation include:

1. Seasonal, or ecological, size variation.
2. Color variation.
3. Morphological variation, both
   - A. Growth anomalies (all of which are abnormalities) and
   - B. Inherited differences, which may constitute
     - (1) abnormal morphological variation, or
     - (2) normal morphological variation.

Size variation.—Over-all size of individual flies appears to be affected markedly by conditions in the larval habitat. Larvae of *Dolichopeza* inhabit mosses and liverworts, which ordinarily grow most luxuriantly in the spring. Adult flies emerge at two times each year, in most species and in most parts of the range of the genus, there being flight periods in the spring and again in the late summer or early fall. Those larvae which give rise to the spring generation of adults feed in the autumn, become quiescent in winter and feed further in early spring, while those developing into adults of the fall generation, being progeny of the spring adults, feed only during a period of about two and a half to three months in the summer, when their moss habitat is usually drier than at other times of the year. That the fall generation adults in all species are of smaller size than those of the spring generation appears to reflect this variation in larval habitat. This is further suggested by the fact that spring generation adults reared in the laboratory, where they are subjected to various inadequacies of environment, are smaller than flies of that generation occurring in nature. Of course, there is size variation among flies of a single generation, which may result from fluctuations in larval environment or may be due to other, less understood causes.

Seasonal variation is well illustrated by *Dolichopeza americana*. On the assumption that wing length is a reliable index of over-all size of the fly, wings of ten males and ten females representing each generation were measured and compared (Table 1). All spring generation flies were captured between 10 and 25 June and those of the autumn generation all on 4 August; and all specimens were collected within the same general habitat, within a radius of 200 yards, at a locality in west central Indiana. The flies were taken

TABLE 1.—Wing Length in *Dolichopeza americana* (Measurements in Millimeters)

	Generation	Mean	Range	Median
Males	Spring	10.3	9.2-11.1	10.4
	Fall	8.4	7.2- 9.1	8.7
Females	Spring	11.4	11.0-12.9	11.2
	Fall	9.4	8.9-10.1	9.2

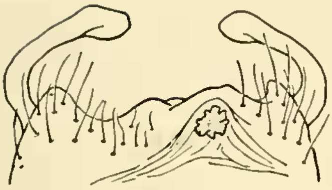
at random from specimens stored in opaque paper envelopes. In this instance, the means in both males and females are widely separated, and it may be seen from the table that the ranges of wing length of spring and fall flies do not even overlap. This is a rather extreme example, but it illustrates the tendency seen in the other species.

Color variation.—Color of preserved specimens is greatly affected by their age, exposure to sunlight, and method of preservation. In specimens only a year or two old, as well as in living material, there is sufficient variation in coloration to indicate that ordinarily no reliance can be placed on slight differences of shade or color for taxonomic purposes. Where I have referred to color in describing species, especially in the key to adult females, I have tried to limit its use to color patterns or to general coloration, used in conjunction with other characters. It is very difficult to communicate one's estimate of color to another person, and because the colors in *Dolichopeza* are not fixed enough to be referred to a standard color guide, it has seemed best to omit discussion of color details.

There are, however, a few examples of significant intra-specific variation in color in North American *Dolichopeza,* the most outstanding of which is that found in *D. walleyi.* This species in general appearance rather closely resembles another, namely *D. sayi.* In northeastern United States and southeastern Canada, where the ranges of the two species broadly overlap, they are distinctly colored. *D. sayi* has darkly spotted thoracic pleura, nearly black stripes on the prescutum, and darkly sclerotized hypovalves in the ovipositor of the female; in contrast, *D. walleyi* has pale thoracic pleura, reddish brown prescutal stripes, and paler hypovalves in the female. Specimens of *D. walleyi* from localities a short distance outside the range of *D. sayi* have coloration suggestive of some sort of mixture of those described, and populations of *walleyi* from Florida, Iowa and South Dakota (that is, from localities furthest from the range of *D. sayi*) are very like *sayi* in the intensity of their markings. This phenomenon has been described as character displacement (Brown and Wilson, 1956).

Growth anomalies.—I have occasionally discovered an individual having a very unusual deformity, which by its rarity and nature appears to be the result of defective development rather than the effect of an unusual gene or combination of genes. In *Dolichopeza tridenticulata,* for example, the posterior margin of the ninth tergum of the male abdomen bears a three-pointed projection such as that shown in Figure 59; but the presence of a foreign particle in the tissue of the tergum resulted in the deformity illustrated in Figure 36. Another growth anomaly is the extraordinary enlargement and sclerotization of the apex of one of the inner dististyles of *Dolichopeza polita,* compared with the normal structure of the opposite appendage in the same individual (Fig. 37). Growth abnormalities may affect any stage in the life history. For example, a pupa of *D. obscura* lacked one lateral lobe of the series of four ordinarily occurring in a transverse row on the eighth sternum (Fig. 38). Above the spiracular region of the larva of *Dolichopeza,* there are four subconical, fleshy lobes, the middle two of which are shorter than the others and situated close together, one at either side of the midline. However, among many hundreds of larvae of all species examined, there was found one specimen in which these two median dorsal lobes had grown together (Fig. 39). This individual, incidentally, showed the normal structure in the next earlier instar. All anomalies of the sort here described have been seen only once among the many thousands of flies examined.

Inherited differences.—Other morphological differences seem to have their basis in the genetic makeup of the insects. Among these are several abnormalities that recur with varying frequencies, either throughout the range of a particular species or scattered throughout the genus. The habitats of *Dolichopeza* are discontinuous in most of the range of the genus in North America, and as a result of this there is probably a great deal of local inbreeding. This, at least, would account for the fact that certain abnormalities are locally quite common. Perhaps the most readily observed of such characters is wing venation, the usual pattern of which in subgenus *Oropeza* is presented, in part, in Figure 40. Now, throughout most of its wide range, *Dolichopeza tridenticulata* has the normal wing venation of this subgenus, but in central and southern Indiana, local populations of this species may have as high as 40 to 55 percent incidence of deformity of the medial field, that is, of the branches of the media. Figures 41 through 47 illustrate wings of *D. tridenticulata* in which deformity of the discal cell, a shift of



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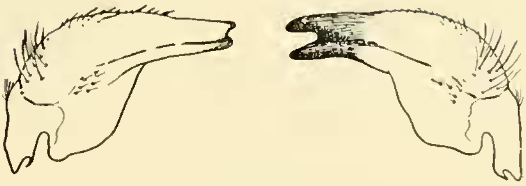

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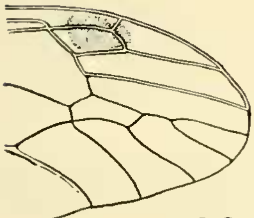

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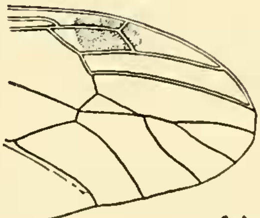

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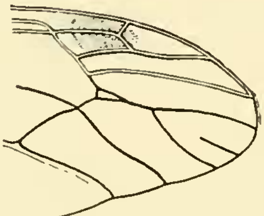

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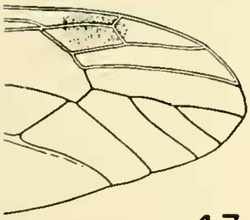

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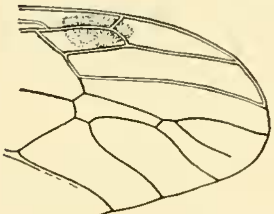

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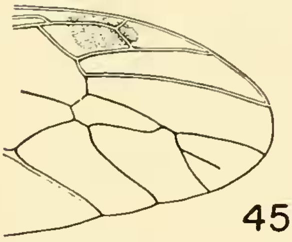

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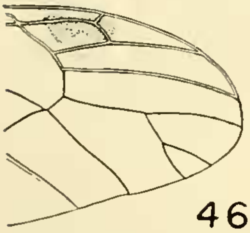

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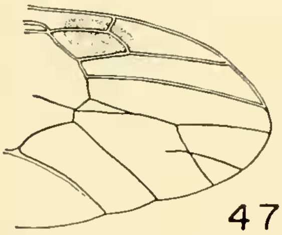

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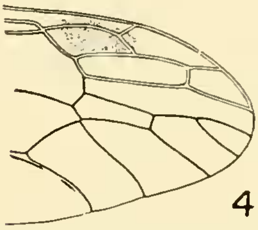

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FIG. 36. Abnormal development of ninth tergum of male *Dolichopeza (Oropeza) tridenticulata* due to presence of foreign body. FIG. 37. Inner dististyles of male *Dolichopeza (Oropeza) polita* ssp., showing abnormal development of apex of left dististyle. FIG. 38. Eighth sternum of pupa of *Dolichopeza (Oropeza) obscura*, showing abnormal development of spinous processes. FIG. 39. Spiracular disc of larva of *Dolichopeza (Oropeza) sayi*, showing abnormal (fused) dorsal lobes. FIGS. 40-48. Variations in wing venation in *Dolichopeza (Oropeza) tridenticulata;* 40—normal venation, 41-47—aberrations of the medial field in a population from central Indiana, 48—spurious cross-vein in cell R_3 in a population from southern Minnesota.

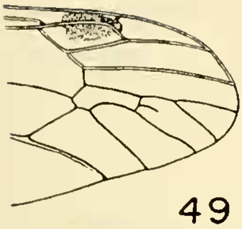
the base of the vein M_2 from M_1 to M_3, and other abnormalities may be seen. Figure 43 is particularly interesting in that the discal cell is completely absent, and the m-cu cross-vein has shifted so as to join the media before its first branching, a combination of characters typical of the venation of the subgenus *Dolichopeza*! Among specimens of *D. subalbipes* from the southern part of the range of the species, there are many similar deformities of the medial field. Some of these, one even resulting in an extra closed cell beyond the discal cell, are shown in Figures 49 through 51.

A further, rather remarkable example of this kind of intraspecific variation is shown in Figure 48. A spurious cross-vein in cell R_3 of the wing is extremely uncommon anywhere in the genus; yet, in one locality in Minnesota, ten *Dolichopeza tridenticulata* in a sample of thirty specimens had such a cross-vein in one or both wings. The venation of these flies was in other respects normal. Venational aberrations of sorts similar to those described here have been observed in the mosquito, *Culex pipiens,* in which species they have been found to be controlled by single mutant genes (Laven, 1957: 452 ff.).

The occurrence of macrotrichia in the apical cells of the wing is similarly uncommon throughout the North American species of *Dolichopeza,* but in *D. walleyi* this variation has appeared in a few populations in scattered parts of the range (Fig. 52).

In contrast to such striking departures from the usual condition, there are several morphological variations of lesser degree that are so often found in almost any population of a species that I think they may be considered as normal variation, just as we recognize certain differences in detail of facial features among normally appearing human beings. These slight modifications of form are probably genetically controlled, although no study of this has been made. Examples are found in all species of *Dolichopeza,* and within each species such characteristics seem to be distributed at random, or nearly so. That is to say, in any population throughout the species' range, all known variations of the particular character may occur. Such differences include minor shifts in the positions of various wing veins with respect to the discal cell (Figs. 53 through 57) and slight modifications of the caudal margin of the ninth tergum or the tergal arms in males (Figs. 58 through 66). Many other examples could be cited, but these will serve to illustrate the point.

Dolichopeza tridenticulata takes its name from the three-toothed projection on the ninth tergum of the male, a structure ordinarily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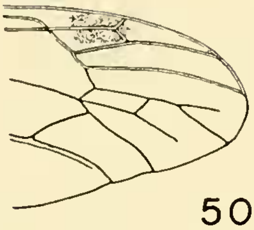
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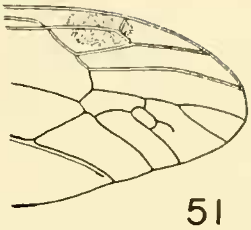
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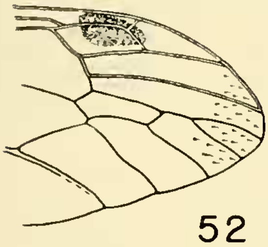
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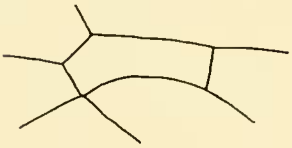
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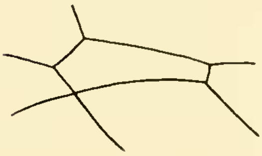
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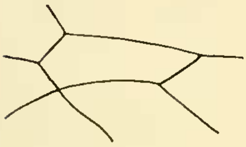
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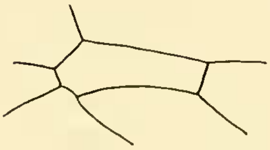
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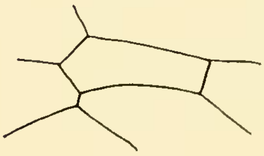
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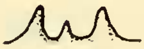
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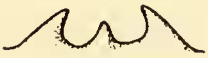
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FIGS. 49-51. Aberrations of the medial field in wings of *Dolichopeza (Oropeza) subalbipes;* 49—specimen from Florida, 50—Georgia, 51—Alabama. FIG. 52. Wing of *Dolichopeza (Oropeza) walleyi* from Michigan, showing macrotrichia in apical cells. FIGS. 53-57. Variations in shape of discal cell (cell 1st M_2 occurring commonly in *Dolichopeza (Oropeza)* spp. FIGS. 58-60. Normal variation in medio-posterior margin of ninth tergum of male *Dolichopeza (Oropeza) tridenticulata.* FIGS. 61-63. Normal variation in medio-posterior margin of ninth tergum of male *Dolichopeza (Oropeza) obscura.* FIGS. 64-66. Normal variation in lateral arms of ninth tergum of male *Dolichopeza (Oropeza) walleyi.*

having a shape like that shown in Figure 59. However, in any sample of several males of this species, one may expect to find the projection more slender, as in Figure 58, or broader and with the points more rounded, as in Figure 60. Likewise, in *D. obscura,* the median posterior teeth of the ninth tergum, most often having the form of Figure 62, may be variously spaced and deflected, as indicated in Figures 61 and 63. Shapes of the apices of the tergal arms in *D. walleyi* may vary as indicated in Figures 64 through 66, not only from one individual to the next but from side to side in the same fly.

In all species of the subgenus *Oropeza,* slight variations in the positions of veins about the discal cell are commonly seen. For example, the m-cu cross-vein may join M_{3+4} (Fig. 56) or M_4 alone (Fig. 57) instead of intersecting the junction of these veins as in Figure 55. A common venational variation in all species of *Oropeza* is the presence of the short segment of the vein M_4 between the discal cell (cell 1st M_2) and the junction with the m-cu cross-vein (Fig. 57). This short length of M_4 has been called the m-cu cross-vein in the nomenclature of Comstock and Needham (see Needham, 1908), who regard the vein M_4 as an anterior branch of the cubitus. Following this system, Johnson often refers, in his descriptions of new species of *Oropeza,* to the presence or absence of the short m-cu cross-vein. Within the *obscura* group, the cross-vein m may cross rather perpendicularly or diagonally from M_{1+2} to M_3 (compare Figs. 53 and 55), and it may be quite short (Fig. 54).

Since these characters may be expected in any sample of several individuals from any locality within the range of a species, and since they appear to have no correlation with geographic distribution and fall easily within the limits of variation of the species, they must be considered as having no taxonomic significance.

In the case of coloration in *Dolichopeza walleyi* already mentioned, the change from one kind to the other is clinal in nature. Not only would it be difficult to distinguish clearly two geographic races, in this instance, but naming them would serve no useful purpose. Variation may not be such a continuous gradation between extremes, however, but rather a regional preponderance of a particular phenotype, or phase. In *Dolichopeza subalbipes,* for example, the lateral arms of the ninth tergum of males are of two types, one with a very slightly expanded tip (as figured by Alexander, 1942: 213) and the other with a greatly enlarged, or inflated, bulbous tip. In the southern United States, the latter form is dominant in all populations, while the narrow tipped form is almost a rarity. In the northernmost states and in Canada, however, the slender tergal arm is much more common. In any one population, both types are likely to occur, so that this cannot constitute either a cline or a subspecific difference. I have seen only a few specimens that seem to be intergrades between the two extremes. On the other hand, if it is possible to demonstrate that the grouping of individuals of a species around two or more means is somehow correlated with geographic distribution, then subspecies may be indicated. In *Dolichopeza polita*, for example, characteristics of coloration, male genitalial structures, and other features of adult and immature forms are generally grouped around three different means, allopatric in distribution but with zones of intergradation at the borders where they meet. These seem to fulfill the requirements of subspecies, as will be discussed later in detail, and it has been found useful in this case to apply names to the three groups.

ADULTS—NATURAL HISTORY

Longevity.—The adult life of *Dolichopeza* is quite brief. Rogers (1933: 29) estimated a maximum duration of adult life of tipulines to be three weeks, but I would judge the maximum for *Dolichopeza* to be little more than half that. Flies kept in the laboratory without food lived from two to four days following emergence, while those that were provided with sugar-water remained alive in some instances as long as six days. The cooler temperatures of natural environments would probably decrease the metabolic rate, allowing the flies to live somewhat longer, and it seems likely that natural sources of nourishment for both the larva and the resulting adult would be a factor in longevity.

Distribution.—Practically the only activities of adult *Dolichopeza* are those related to reproduction. These are discussed in detail in the sections on mating behavior and oviposition which follow. But the geographical, ecological and seasonal distribution of species of *Dolichopeza* present certain problems possibly bearing on reproductive activities. It seems not unreasonable to expect that if species are very closely related there might be occasional flow of genes between them, unless they are somehow wholly isolated from each other. Most species of North American *Dolichopeza* fall together with one or more other species into groups with very close interrelationship, the species in some instances so nearly identical as to be distinguishable only by microscopic examination. This being the case, it becomes important to know if there is cross-mating between any two recognized species, either regularly, occasionally, or at all. If there is any exchange of genetic material of one kind of *Dolichopeza* with any of its relatives, it must of course take place in the adult stage. Consequently, it is worthwhile to know what opportunities these flies have for cross-mating; that is, where do the adults of the different forms meet and intermingle geographically, ecologically and seasonally?

That there is some ecological separation of the species has already been indicated (p. 672). Darkly-colored species are usually taken in deeply-shaded situations, and those having various patterns of dark on buffy yellow are usually found in the more open shade of forest and marsh vegetation. The general environment itself can be divided into three categories, insofar as *Dolichopeza* is concerned; these are rocky gorges and ravines, forests, and marshes, bogs and swamps. Even where these broad types of habitats meet, as where rocky gorges occur in forests, the species of *Dolichopeza* demonstrate a marked degree of ecological separation.

It is, of course, the microhabitat that determines the presence or absence of a species. It is nevertheless possible to divide the North American species into three groups, based upon the three major kinds of habitats named, for within these habitats occur the microenvironments that meet the particular needs of the species. Characteristic of rocky gorges and ravines of the Appalachian Mountains are *Dolichopeza americana, carolus, johnsonella, obscura, polita, tridenticulata, walleyi,* and, depending on the part of the mountains, *subvenosa* or *venosa.* Of these, *carolus* and *walleyi* are more specifically associated with leafy vegetation along the sides of the ravines, while *subvenosa* or *venosa* are found either in such vegetation or together with the other species in nearly any deeply-shaded crevice or cranny. The same association of species is found west of the Appalachians in places where irregularities in the terrain afford conditions similar to those of mountainside ravines, except that *subvenosa* is replaced by *venosa.*

In cool, mesic forests, the favorite haunts of *Dolichopeza obscura, walleyi* and sometimes *tridenticulata* and (within its range) *subvenosa* are hollows in standing or fallen trees, cavities beneath outcropping rocks, undercut banks, or about the roots of windthrown trees, but *walleyi* may occur also out among the lower plants, where *subvenosa, venosa* and *carolus* are sometimes found.

Those species encountered most often in bogs, swamps and marsh borders include *Dolichopeza dorsalis, sayi, similis* and *subalbipes,* although such habitats are commonly occupied also by *obscura* (again seeking out the deepest shade) and sometimes by *americana.*

Data on seasonal distribution of adults are based mostly upon dates of capture. I have not often worked in one locality long enough to learn precisely the order of appearance of each species and how long it was present as adults. Observations made in 1953 at a particular cavity in a rock cliff in Turkey Run State Park, Parke County, Indiana, showed *Dolichopeza americana* to be the earliest species, appearing on 18 May and reaching a spring peak of population about 26 May. *Dolichopeza polita* ssp. first appeared on 23 May and reached a relatively high peak, exceeding the numbers of all other species together, on the 29th and 30th of May. On the 28th of May, *D. walleyi* and *obscura* were found with the others, but in much smaller numbers. Four days later, *tridenticulata* appeared, making five species represented in the sample of 142 flies taken on 1 June from that one rather small cavity, which had perhaps ten or twelve square feet of roof surface from which the flies were suspended. All these were taken with a single sweep of the net, and at other times it was possible to take a sixth species in the same place, together with the five named.

It will possibly occur to the reader that this is an unusual situation and that localities in which several species of *Dolichopeza* exist side by side as adults are really uncommon. But the fact is that what I have described for the Indiana locality can be duplicated in many parts of the North American range of the genus. (And in Korea, in a rather similar environment, I found four species of *Dolichopeza* together in crannies of a cliff in early June.) The following data from my own collections will bear out this statement:

Ohio, Portage County, Nelson Ledges State Park, 24-25 June 1953: *americana, carolus, johnsonella, polita* ssp., *subalbipes, tridenticulata, venosa* and *walleyi.* On another trip to this place I took also *obscura.* Total: 9 species.

Virginia, Rockingham County, Dry River, 6 July 1952: *americana, carolus, obscura, tridenticulata* and *walleyi.* Total: 5 species in a sample of 12 specimens taken in about ten minutes of collecting just before a rainstorm.

North Carolina, Burke County, Linville Falls, 14 June 1958: *americana, carolus, obscura, polita* ssp., *subvenosa, tridenticulata* and *walleyi.* Total: 7 species among 27 specimens collected.

Georgia, Union County, Neel's Gap, 10 June 1958: *americana, carolus, johnsonella, obscura, subalbipes, subvenosa* and *tridentic-*

ulata. In a collection made at this place on 28 June 1952, I took also *polita* ssp. and *walleyi.* Total: 9 species.

Virginia, Giles County, near Mountain Lake Biological Station, 21 June 1958: *americana, carolus, obscura, subalbipes, subvenosa, tridenticulata* and *walleyi.* Other collections at this locality yielded also *johnsonella* and *polita* ssp. Total: 9 species.

Maine, Cumberland County, near Bridgton, 1 July 1953: *americana, obscura, sayi, subalbipes* and *walleyi.* Total: 5 species among 7 flies of the genus found.

West Virginia, Pocahontas County, Droop Mountain Battlefield State Park, 23 June 1958: *americana, johnsonella, obscura, tridenticulata* and *walleyi* all together among the rafters of one picnic shelter. In the same state and county, a few miles away in Watoga State Park, 5 July 1952: *americana, carolus, obscura, polita* ssp., *subalbipes* and *tridenticulata.*

Pennsylvania, Luzerne County, Ricketts Glen, 10 July 1952: *americana, carolus, johnsonella, obscura, polita* ssp. and *tridenticulata.* In four different collections, here, in three different years, I have never found *walleyi,* but I am confident it will be added to the list.

Ohio, Hocking County, "Neotoma" (a small valley near Rockbridge belonging to Dr. Edward S. Thomas of the Ohio State Museum), 30 May 1952: *americana, carolus, obscura, polita* ssp. and *tridenticulata.* On other occasions, I have also taken within this limited area *dorsalis, johnsonella, subalbipes, venosa* and *walleyi,* making a total of 10 species.

Great Smoky Mountains National Park (collections in Sevier County, Tennessee, and Swain County, North Carolina), 30 June 1952: *americana, carolus, obscura, polita* ssp., *subalbipes, subvenosa* and *tridenticulata.* Also taken in the park are *dorsalis, johnsonella* and *walleyi.* Total: 10 species.

Michigan, Washtenaw County, Mud Lake Bog (near Whitmore Lake), various dates: *americana, dorsalis, obscura, sayi, similis, subalbipes* and *walleyi,* often four or five species in any one collection.

Michigan, Livingston County, Edwin S. George Reserve (a natural area belonging to the University of Michigan, near Pinckney), various dates: the same species list as for Mud Lake Bog, except that *venosa* is added. Total: 8 species.

Wisconsin, Juneau County, Rocky Arbor Park (near Wisconsin Dells), 6 July 1950: *carolus, obscura, polita* ssp., *subalbipes, tridenticulata* and *venosa.* Total: 6 species.

Kansas, Douglas County, 15 miles south of Lawrence, 30 August 1957: *obscura, polita* ssp. and *walleyi.* These three species are from a locality that is probably near the western limit for the genus, at this latitude.

A great many more collection records similar to those presented here, particularly from the Appalachian region, could be mentioned, but these suffice to illustrate the point that where one species of *Dolichopeza* occurs, one or more others are likely to be found with it.

With two exceptions (*similis* and *venosa*), all the species of *Dolichopeza* that occur in eastern North America appear to have two generations per year in that part of their range lying roughly between the latitudes of northern Florida and New England. In Florida and southernmost Georgia, there are records of some species for nearly all months of the year, suggesting that the life cycle is repeated as often as biologically possible, with perhaps a dormant period in January and February of some years. While there seems to be no particular peak of abundance of individuals of any species at any season, in the Florida region, most of the collection records indicate that early summer (June) is a time when the numbers of most of the species are increased. From Georgia northward, particularly at higher elevations, there occurs a marked two-generation cycle, annually. In general, the peaks of emergence of adults come in late May and early June and again in August, but early and late emergence of individuals give considerable slope to these peaks. Available collection records from the northern edges of the range of the genus are insufficient to give a clear picture, but they suggest that a single mid-summer generation is the usual thing. Further collecting is needed especially in Canada to verify this. *Dolichopeza similis* and *D. venosa* are northern species, found only in the northeastern states and Canada, with a flight period from late May to early August, nearly all the records being for June and the later records being for the more northern parts of the range. More specific data on dates and localities of collections of adults will be found listed in the sections on the species concerned.

Activities.—Certainly the most spectacular activity of adults of *Dolichopeza* is their peculiar dancing flight. This is most easily observed in species of the *obscura* group because, somewhat restricted to certain niches by their reaction to the intensity of outside light, they will leave their darkened shelters by day only when greatly alarmed. Dropping from its resting position, the fly moves in a rather elliptical path, first downward and backward, then rising and forward, keeping the head oriented more or less toward the original point of suspension. This cycle is repeated with such rapidity that the fly seems almost to fade from view, although the dance is limited to about a three-inch ellipse. The dance of *Dolichopeza carolus* is more conspicuous, mostly, I suppose, because of the paler colors of that species, which contrast somewhat with its leafy habitat. When disturbed from a distance, *carolus* moves in a more vertical ellipse, often six inches in length; but if approached closely, it usually moves away rather directly and hurriedly. It is my impression that the other species that are found most commonly in vegetation also take readily to flight when disturbed. This is particularly true of *dorsalis* and *sayi,* and I have never observed the elliptical flight in either of these species. Among the species of the deeply shaded, rock gorge habitat, those of the subgenus *Oropeza* seem much more restless than *D. americana;* they are more easily alarmed to the point of dancing and are slower to settle back to rest, and in the same respects, males are more restless than females. Spontaneous dancing during twilight formation of swarms, possibly related to mating activities, has been noted in *Dolichopeza johnsonella.* The dance of this species in the open air was observed to be nearly straight up and down, along a fairly constant path of about twenty inches in length, and the flight was markedly slower than that of the diurnal dance beneath a rock ledge.

During the daylight hours, the primary occupation of adults of *Dolichopeza* is resting in such shaded and protected haunts as are available within the general habitat. In repose, the flies almost invariably hang from some overhead support, such as the bottom of an outcropping rock, an undercut bank, the roof of a darkened drain tile or culvert, stems or leaves of low plants, or the eaves of buildings situated among trees. It has been observed that the number of legs used in suspension varies. Alexander (1919: 929-930) states that a point of distinction between the subgenera is that "*Oropeza* hangs . . . with only the fore legs attached . . . *Dolichopeza,* on the contrary, has the four anterior legs on the support, the hind legs dangling. . . ." I think this was a slip of the pen, for while one may observe considerable variation in the resting postures of both subgenera, it is *Dolichopeza americana* that is nearly always seen suspended by the two front legs only, with the four other legs held out to the sides, perhaps dangling a bit (Fig. 67). Species of *Oropeza,* on the other hand, usually hang by both the prothoracic and mesothoracic legs (Figs. 68-70). Variations involving three to six legs are not uncommon in both subgenera. In fact, among more than a hundred *Dolichopeza* (*O.*) *polita* ssp. observed in an Indiana locality on two days in late May,

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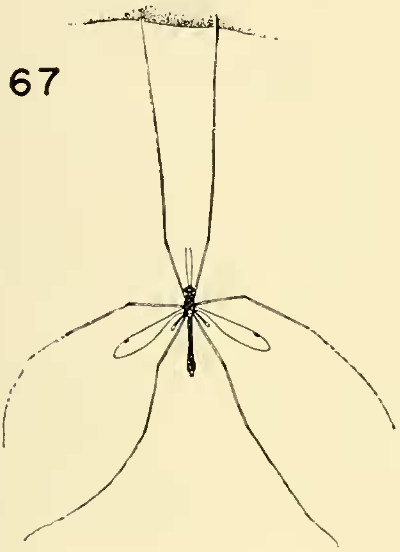

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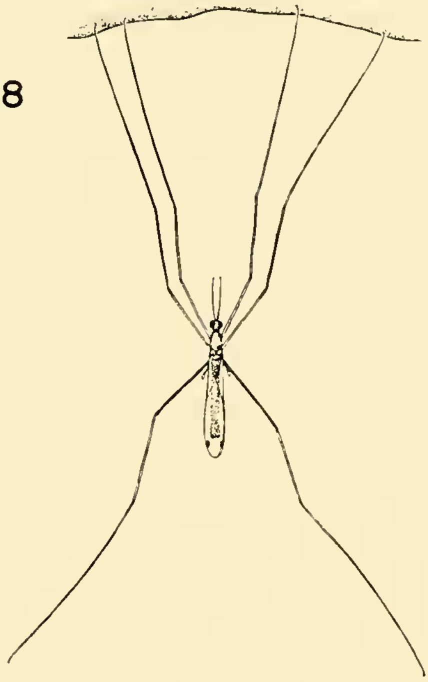

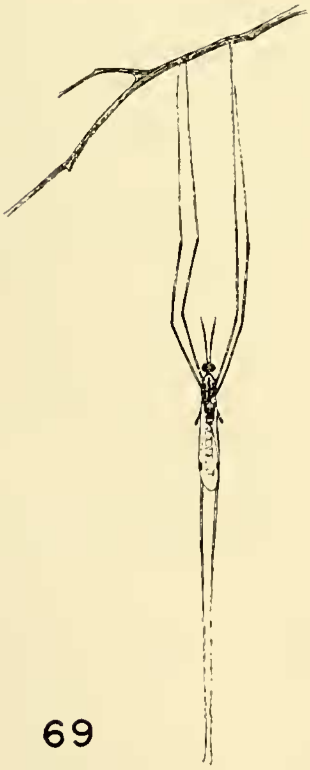

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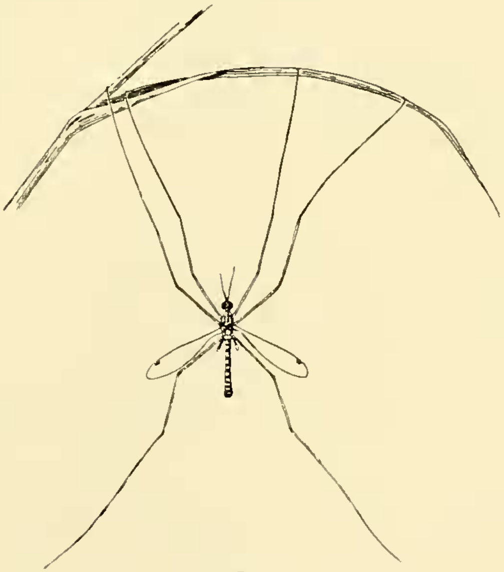

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FIG. 67. Resting posture of *Dolichopeza (Dolichopeza) americana.* FIG. 68. Resting posture of *Dolichopeza (Oropeza) polita* ssp. (also of *johnsonella, obscura* and *tridenticulata*). FIG. 69. Resting posture of *Dolichopeza (Oropeza) carolus* (also of *subalbipes, subvenosa* and *venosa*). FIG. 70. Resting posture of *Dolichopeza (Oropeza) sayi* (also of *dorsalis*).

nearly all were suspended by all six legs, whether from an upside-down horizontal surface or on a more or less vertical surface, and whether single individuals or mating pairs. Commenting on this behavioral difference, Alexander (1920: 982) says "the resting positions of *Dolichopeza* are described . . . and the striking dissimilarities to *Oropeza* noted. It may be that *Oropeza* is not so close to *Dolichopeza* as has been believed." Certainly these two subgenera represent distinct natural groups, but the difference in behavior appears to be no more than a consequence of a morphological dissimilarity that is much less remarkable than the difference in genitalia or wing venation. Comparing several specimens each of *D.* (*D.*) *americana* and *D.* (*O.*) *tridenticulata,* species of about equal size, I found the ratio of the length of the prothoracic leg to that of the mesothoracic leg to be greater in the former species. In both these species (as also in other species of *Oropeza*), the prothoracic legs slightly exceed the length of the second pair, but the difference in total length is perhaps significant. The ratios for *americana* and *tridenticulata* were 30.5:27.9 mm. and 30.7:29.0 mm., respectively, there being a greater difference in *americana* that might explain its peculiar posture.

The position of the wings in repose is of interest, as there is some correlation with the grouping of species on the basis of coloration, noted earlier. It has been stated that *Dolichopeza americana* rests with its wings outspread and that species of the subgenus *Oropeza* fold their wings over the body when at rest. But this is true only in part. *Dolichopeza americana* (Fig. 67) does rest with its wings apart, a posture that is unique among those species preferring the deep shade, but it is my observation that the swamp inhabiting *D. dorsalis* and *sayi* nearly always rest with their wings outspread and tilted somewhat forward, as they hang among the grasses and stems (Fig. 70). *Dolichopeza johnsonella, obscura, polita* sspp., and *tridenticulata,* flies which seek the deepest shade by day, all fold their wings over their backs and rest with the hind legs dangling out to the sides (Fig. 68). *D. walleyi* is also often seen in this position, especially when concealed in dark recesses, but when out among low plants beneath the trees, it often rests with the wings outspread, a peculiar correlation of variable behavior with different environment. *D. similis,* a swamp dweller usually found among low plants, also exhibits considerable variation in wing position when at rest but usually assumes a resting posture like that shown in Figure 68. A most unusual situation in regard to resting posture is that of *Dolichopeza carolus, subal-*

bipes, subvenosa and *venosa.* Morphologically, *subalbipes* belongs to the *obscura* group and the other three species to the *sayi* group, yet in general coloration and size they are very similar. The commonest environment of each is leafy vegetation in damp, shaded places, although usually no more than two of the four species occur together in the same habitat. The resting postures of these very similar species are identical and at the same time different from those of all other North American species of *Dolichopeza.* They hang by the front two pairs of legs, with the wings folded over the body and the hind legs held almost straight downward and quite close together (Fig. 69), a position that conceivably has some camouflaging effect, judging from its occurrence throughout this group of convergent species.

Reaction of resting flies to changes in light intensity has been noted a few times. Rather regular observations were made of adult *Dolichopeza* congregated in a recess in a sandstone cliff at Turkey Run State Park, Parke County, Indiana. In late May, this hole is well shaded through most of the day and often contains as many as three hundred flies of various species. About five o'clock in the afternoon, however, sunlight strikes the sandy floor of the cavity and by reflection somewhat illuminates the roof, causing the resting flies after a time to move. Under such circumstances, they usually retreat deeper into their crannies and in this case crowded into a small adjoining hole that was only about eight inches high, with perhaps two square feet of roof. In this small but dark retreat I once found about two hundred flies, that is, nearly a hundred per square foot of area available for suspension. At other times, I found that when I reflected sunlight into resting sites, species of *Oropeza* reacted readily, while *D. americana* responded slowly or not at all. When the sky becomes dark with clouds, in the daytime, many *Dolichopeza* leave their shaded hiding places and fly about among the low plants of the woods, but I have also noticed that at such times those remaining at rest are less easily disturbed by the presence of humans than at other times. For example, on one dark, cloudy day resting flies showed no reaction to the presence of my hand held only half an inch from them or slowly circled around them. They took flight immediately, however, in response to a slight touch.

Although Dolichopezas rest quietly during the day, they range rather widely by night. Along McCormick's Creek, in Indiana, I have watched *johnsonella* and other species of the *obscura* group, on a June evening, moving from beneath the limestone ledges out into nearby trees. In the gathering dusk, they could be seen dancing in mid-air among the trees in the ravine and high up on the face of the cliff. At other times and places, I have observed *D. americana* and *polita* ssp. still at rest a few minutes after darkness, but there is every indication that most *Dolichopeza* are away from their daytime haunts during most of the hours of darkness. It is a common thing to find crannies where hundreds of them rest by day to be quite empty after nightfall. At daybreak, along forest trails, one may find the flies making their way back to darkened shelters. In northern Michigan, I have waited beside an empty daytime resting place of *tridenticulata*, in the early morning, and watched the flies returning from all directions as the sun rose. Further evidence of nocturnal wandering by *Dolichopeza* is found in captures of occasional specimens at light traps (notwithstanding their tendency to avoid the brighter light of the sun), or the finding of flies in temporary structures affording shade from the rising sun (such as tents in a campground), in places far from their diurnal haunts. It is possible that during such excursions away from the protection of daytime habitats, individuals are caught up in high winds and carried to other localities, there to establish new populations of the species.

Although the fairly well developed digestive system of the adult *Dolichopeza* suggests that the flies do some feeding during their short existence, I have only once seen one so occupied. This was *Dolichopeza americana*, seen drinking at a shallow pool of seepage water on a mossy, horizontal ledge of sandstone. The fly stooped, somewhat in the manner of a drinking giraffe, with its head down and tail end elevated, its legs rather evenly outspread. I have no idea what natural foods are utilized, but in the laboratory the flies fed upon thin sugar syrup, which was held in shreds of paper tissue hung upon the sides of the cage. Speaking of crane flies generally, Rogers (1933: 30) says, "Nearly all species that have been reared were able to mate and oviposit without food, and, although feeding practically doubles the life of the adults and tends to prolong somewhat the period of oviposition, lack of food does not appear to decrease the number of fertile eggs oviposited." While my records do not show a doubling of adult life time among flies given food, an increased life span is indicated; and I find no effect of food or lack of it on the fertility of eggs or the period of oviposition by female flies in captivity.

Predators and parasites.—There are no specific records, so far as I am aware, of predation on *Dolichopeza* by a vertebrate or large invertebrate, although Alexander (1920: 721 ff.) presents a formidable list of known enemies of crane flies generally, many of which are certainly potential and probably actual predators of *Dolichopeza*. While probing the darkened recesses occupied by these flies, I have occasionally encountered a small salamander or a toad; and it is not an uncommon sight to see a large dragon fly working along a cliff, now diving into a shaded niche, now backing out and flying to another. I once found an ant attacking an emerging *Dolichopeza obscura* that was only partly out of its pupal skin. Swamp species of *Dolichopeza* are undoubtedly picked up by foraging birds, especially at times when they constitute a large fraction of the flying insects present.

It has been remarked that some species of *Dolichopeza* have ". . . a notable predilection for resting on spiders' webs." I would rather say that they often find their chosen resting places occupied also by spiders, from whose webs they are able to hang without often becoming entangled. That Dolichopezas do fall prey to web-spinning spiders, as well as to cursorial ones that stalk them in their crannies, is shown by the following list of spiders collected with their prey:

Dolomedes sp. (immature) with *Dolichopeza* (*O.*) *obscura;* Michigan, Cheboygan Co., Douglas Lake, 6 July 1949.

Philodromus marxii Keyserling with *Dolichopeza* (*O.*) *polita;* Illinois, LaSalle Co., Starved Rock State Park, 7 July 1951.

Meta menardi Latreille (immature) with *Dolichopeza* (*O.*) *tridenticulata;* Indiana, Owen Co., McCormick's Creek State Park, 24 June 1950.

Theridion tepidariorum C. Koch with *Dolichopeza* (*O.*) *polita;* Michigan, Eaton Co., Grand Ledge, 16 August 1951 (three flies in one web).

Theridion tepidariorum with *Dolichopeza* (*O.*) *tridenticulata;* Illinois, LaSalle Co., Starved Rock State Park, 7 July 1951.

Theridion tepidariorum (immature) with *Dolichopeza* (*O.*) *johnsonella;* Indiana, Owen Co., McCormick's Creek State Park, 20 July 1951.

Theridiosoma radiosum McCook with *Dolichopeza* (*O.*) *tridenticulata;* Indiana, Owen Co., McCormick's Creek State Park, 12 June 1951.

Theridiosoma radiosum with *Dolichopeza (O.) obscura;* Indiana, Parke Co., Turkey Run State Park, 19 June 1950.

Theridiosoma radiosum with *Dolichopeza* (*O.*) *polita* ssp. and *Dolichopeza* (*O.*) sp.; Indiana, Parke Co., Turkey Run State Park, 11 June 1951 (three records).

Uloborus americanus Walckenaer with *Dolichopeza (O.) tridenticulata;* Iowa, Clayton Co., near Guttenberg, 8 July 1951.

The following portion of a letter from Dr. Willis J. Gertsch, who identified all the spiders, is of interest: "The *Dolomedes* is a three-clawed vagrant spider which ordinarily runs over the ground or low vegetation, most often near water. The *Philodromus* is also a vagrant and may be seen on the ground, but is rather more frequently swept from herbs and shrubs. The remaining species are all sedentary forms. The *Theridion* is the very common cosmopolitan house spider. The *Theridiosma* spins an unusual orb web and usually is associated with shaded woods. The same is true of *Meta,* also an orb weaver which favors dark woods and is even partial to caves. *Uloborus* is one of the cribellate orb weavers and makes a beautiful horizontal web."

It so happens that all the records above involve flies of the *obscura* group that frequent rocky crevices and crannies. This fact is related partly to the greater ease with which predation is observed in such habitats and partly to my confessed preference for working in these more comfortable places. I have no doubt that the swampland species of *Dolichopeza* have many spider predators also. It should be added that *americana, carolus, walleyi* and *similis* have been found in the webs of spiders, but in these instances I was unable to find the spiders.

While external parasites probably seldom kill a crane fly, they do sometimes cause their host to become shriveled and undersized (Rogers, 1942: 57). All species of *Dolichopeza* are occasionally afflicted with mites, and as many as eight or ten on a fly is a common thing. The heaviest infestation I have found was a group of 98 mites clustered mostly on the abdomen of a male of *Dolichopeza venosa,* taken in Eaton County, Michigan. The mites usually attach to some part of the thorax, often to the abdomen, and rarely to proximal parts of the legs, but I have never found them attached to the head or wings. Two kinds of mites are the most frequent ectoparasites of *Dolichopeza.* One is a plump, reddish or orange colored erythraeid (Acarina: Erythraeidae) of undetermined genus. The other is a somewhat flattened stigmaeid, identified by Dr. Joseph Camin as belonging to the genus *Ledermüelleria* (Acarina: Stigmaeidae). Actually, there may be two species of this genus parasitic on *Dolichopeza,* as those on some flies are of a rusty orange color, while others on other flies are mottled tan or gray. Their body form is depressed, the dorsum broadly curved and the ventral surface slightly concave.

Only one instance of nematode endoparasitism of adult *Dolichopeza* has come to my attention. This was a male of *Dolichopeza tridenticulata,* collected in Shenandoah National Park, Virginia, on 28 June 1958. Although the total body length of the fly was only 11 mm., the nematode measured almost 35 mm. in length. The parasite was looped from end to end of the fly's abdomen four complete lengths, and its head was inserted far into the thorax of its host. In spite of this condition, the fly was taken on the wing, and its digestive and reproductive organs, on dissection, appeared intact and capable of functioning.

On two occasions, I have found larval Tachinidae endoparasitic in adult *Dolichopeza.* Dissection of the abdomen of a male *Dolichopeza carolus* taken in Neel Gap, Union County, Georgia, 28 June 1952, revealed two small dipterous larvae identified as tachinids. On 6 June 1960, at Cumberland Falls State Park, Whitley County, Kentucky, I captured a female *Dolichopeza tridenticulata* with a peculiarly bulging abdomen. Unfortunately, I did not notice this enlargement until after the fly had been killed in the cyanide jar and the 3.5 mm. long tachinid parasite was forcing its way out of the abdominal cavity through the pleural membrane. Dissection showed the vital organs of the host intact, so it seems likely that the tachinid had fed chiefly on the fat tissue and perhaps the haemolymph.

MATING BEHAVIOR

It is probable that in most species of *Dolichopeza* mating usually occurs during the night, although in certain species pairs are not uncommonly found still in copulation well into the following daylight hours; and occasionally matings are commenced during the day, especially if the light intensity is low, as when the sky grows dark before a summer thunderstorm. As suggested earlier, late evening swarming noted in a few species may be a preliminary to mating, but it is not possible at this time to say what pre-mating activities are typical for the genus under natural conditions. Observation of diurnally mating pairs and those artificially illuminated in the laboratory provides the only exact information on mating behavior, the basis of the following descriptive comments.

Attracted to the same shaded daytime resting sites, males and females are brought into close proximity but appear to ignore one another unless actual physical contact, usually of tarsi, occurs. Now and then, when a resting group of flies is disturbed and is set into dancing motion, a male may attempt copulation with one or more females before settling to rest again. Unreceptive females, in the case of *Dolichopeza polita* ssp., have been seen to respond to these attentions by fluttering their wings and kicking their hind legs over their backs. If a female is receptive, however, she moves her wings slightly apart and remains quietly suspended, while the male hovers over her, curves his abdomen down alongside hers, and reaches from below or behind to gain a grip upon the ovipositor with his dististyles (Fig. 71). I have observed these reactions, with minor variations, also in *Dolichopeza americana, sayi, tridenticulata* and *walleyi* and suspect that they are rather uniform throughout the genus.

During copulation, the female ordinarily supports the weight of both flies, as the male hangs head downward, held fast by the grip of his genital appendages (Fig. 72). Seen from the side, the legs of the flies are not arranged generally in one plane as they might seem from the figure. The fore and hind legs of the male are held out somewhat dorsally with respect to the fly's body and the mesothoracic legs somewhat ventrally. The hind legs of the female (and the middle legs, in the case of *americana*) are deflected in a similar manner. In *americana,* the wings of both partners are held out to the side, but in *Oropeza* spp. the female normally keeps her wings folded over her back, while the male holds his wings outspread. Because of the manner of coupling, suspended mating pairs are so oriented that the dorsal surface of the male and the ventral surface of the female face the same direction. If both members of the pair are clinging to some support, as often happens, their abdomens are variously revolved to maintain the proper clasp. Each may rotate the abdomen 90 degrees, or one may twist 180 degrees, etc.

The following is the usual arrangement of the copulatory structures in mating: The male grasps the female genital segments from below or behind, his outer dististyles getting a loose hold about the tenth tergum. When the hypovalves of the female have been maneuvered into the male's genital chamber, he closes the tips of the inner dististyles into sclerotized folds on the dorsal or inner surfaces of the hypovalves. This provides the firm grasp that is so strong as to allow mating pairs to take to the wing, when alarmed, and not become separated. It may be seen in Figure 73 that the pressure of the tergal arms on the edges of the hypovalves serves to brace them securely against the underside of the ninth tergum of the male, while the gonapophyses force the tenth tergum and cerci apart from the hypovalves. This wide separation of upper and lower elements of the ovipositor exposes the opening to the bursa copulatrix, into which the penis is inserted, as indicated by dotted lines in Figure 73. In *Dolichopeza americana,* the absence of tergal arms seems compensated by a shift dorsad in the position of the inner dististyles, which hold the hypovalves well apart from the cerci. The specific configuration of the medio-posterior margin of the ninth tergum of the male does not seem to have any functional significance.

Although I have never observed males waiting beside female pupae, as described by Alexander (1919: 881) for several other

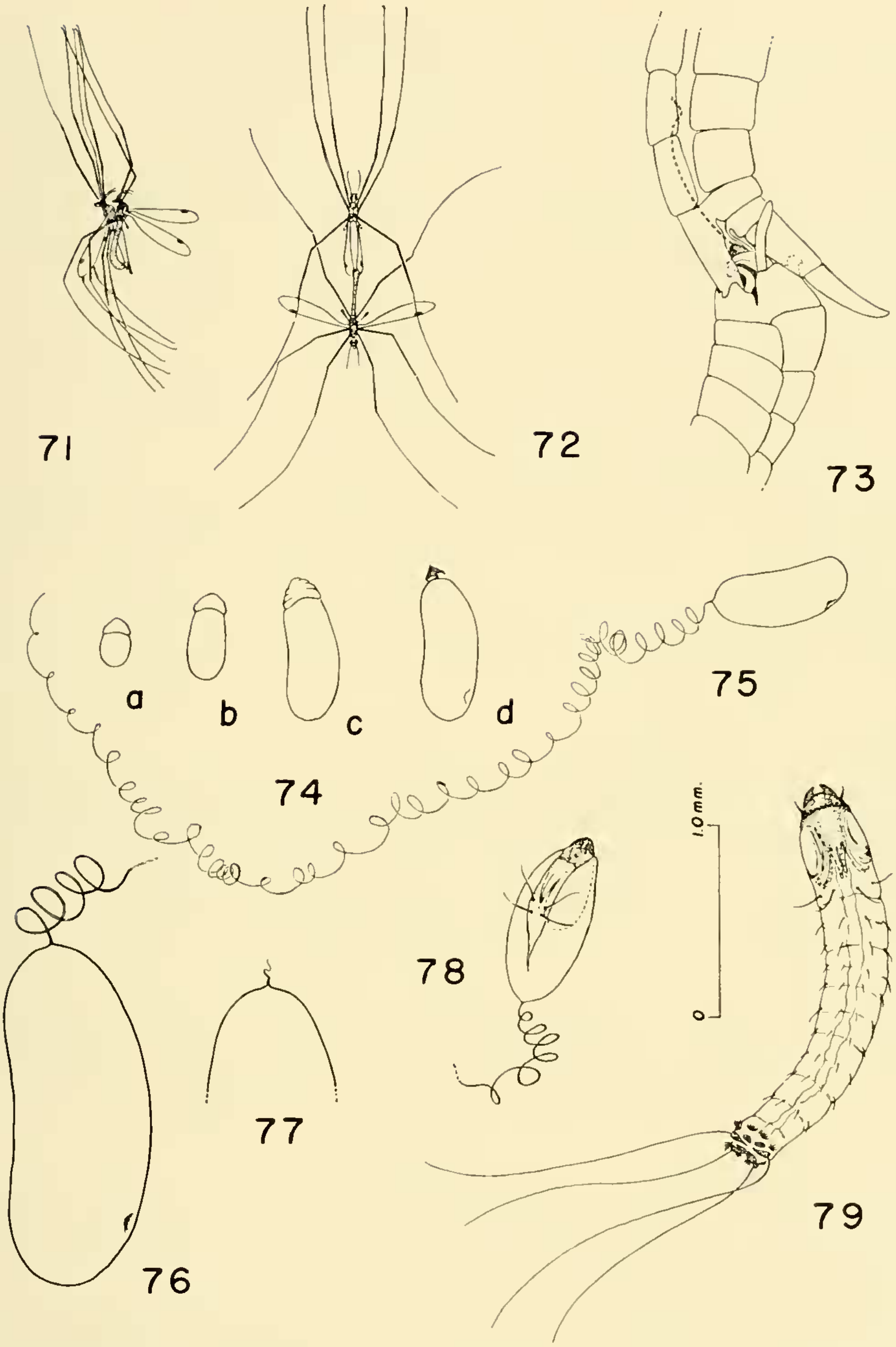


FIG. 71. Position of male (shaded) and female (not shaded) *Dolichopeza (Oropeza)* sp. preliminary to mating. FIG. 72. Same as 71 but showing position in mating. FIG. 73. Detail of hypopygia of male and female *Dolichopeza (Oropeza)* sp. in mating. FIG. 74. Stages in development of egg of *Dolichopeza (Oropeza)* sp.; a-c—immature eggs, showing cap of cells from which terminal filament develops, d—mature egg, showing coiled terminal filament. FIG. 75. Egg of *Dolichopeza (Oropeza)* sp. with terminal filament uncoiled. FIG. 76 same as 75, enlarged, showing micropyle. FIG. 77. Egg of *Dolichopeza (Oropeza) polita polita,* showing vestigial terminal filament. FIG. 78. Hatching of egg of *Dolichopeza (Oropeza)* sp. (scale pertains to Figs. 78 and 79 only). FIG. 79. Larva of *Dolichopeza (Oropeza) obscura,* first instar, 48 hours after emergence from egg.

genera, I do believe that females are somehow found by males and mated with very soon after emergence. Mating pairs frequently involve teneral females whose abdomens are still soft and show the greenish color of the immature stages. As emergence almost always occurs during the hours of night, it is somewhat of a problem to understand just how males and females come together (compare with above description of daytime mating activities). To learn more about nocturnal behavior of these flies, I have made many trips to known larval and pupal habitats, and, using an electric lantern, watched for emergence and subsequent mating. In no case did I find mating to take place near the pupal site, so I assume that some amount of flight is involved in bringing the two sexes together. Mating appears to take place usually at some distance from diurnal resting sites, for these are nearly always vacant at night. In northern Michigan and in Indiana, however, I have found many mating pairs of *Dolichopeza tridenticulata* beneath the eaves of sheds, at about midnight, where earlier in the day only single flies could be found.

In dimly-lit rock gorges and other similar places, one may find mating pairs, here and there, nearly any time of day, in season; but almost all pairs of the majority of species were observed to separate by mid-morning. Mating pairs of *americana* and *polita* sspp., however, are often found during the daylight hours. In Clifty Ravine, Jefferson County, Indiana, on 3 August, I found hundreds of mating pairs of *americana*, at nine o'clock in the morning, when the hazy sunlight had not yet become bright through the trees. Almost no unmated individuals were seen. This same situation was found again, about noon of the same day, in Muscatatuck State Park, Jennings County, Indiana. At Nelson Ledges State Park, Portage County, Ohio, dozens of mating pairs of *polita* sspp. were collected in the hour just before noon on 14 July.

The duration of mating is not known, but the pairs of *americana* and *polita* mentioned seemed to have been formed during the previous night, that is to say at least six to eight hours before the time of observation. In the laboratory, pairs of *walleyi* and *sayi* remained in copulation for as long as eight hours, and under natural conditions a pair of *tridenticulata* was observed together at sunrise and for three hours thereafter.

It is probable that mating takes place throughout the egg-laying period, which lasts about three or four days, perhaps longer in some females. When flies were confined to close quarters in the laboratory, mating sometimes occurred on three successive nights.

Females from mating pairs collected in the field frequently are found to contain only a few eggs, suggesting at least one prior mating.

It would seem that among closely-related species living so near to one another that there might occur frequent matings or attempted matings in which the partners are of different species. However, I have never observed this to happen. Among many hundreds of mating pairs observed or collected, not one was found to involve two species. A male of *Dolichopeza carolus* was once found apparently attempting to gain a copulatory hold on a female of *americana* that was already mated with a male of her own species; and I have seen, in dense, dancing swarms of several species, males very briefly approaching females of another species but never going so far as to secure a grasp with the hypopygium. It is understandable that size differences would serve as a barrier to cross-mating, in some cases, as between males of *polita* and females of *americana* often found sharing the same resting sites. But among adults of many other species that come into actual contact or near contact there are no such obvious barriers to cross-mating. The genitalial clasp is general in nature, far from the complex "lock and key" interrelationship described for some insects, and appears to be essentially the same among many species observed. But it is more significant that cross-matings seem in general not even to be attempted. Accordingly, it must be that by means of some sense as yet unknown the flies are attracted to mates of their own kind and either repelled or at least not attracted by other species, no matter how closely the two may apparently be related.

OVIPOSITION

In the laboratory, oviposition occurred almost without exception during the night and was never observed by day. Neither have I ever seen females of *Dolichopeza* in their natural surroundings behaving during daylight hours as if they were laying eggs. However, on a few occasions females of *polita, tridenticulata* and *walleyi* were seen ovipositing during late evening, just before the dark of night. These females were flitting up and down cliff faces, flying very close to the thin carpet of mosses that covered the rock. After a time of seemingly random movement (it is possible certain mosses were being sought), a given female fly would commence a series of bouncing motions over an area of moss perhaps four inches in diameter. The bouncing action is accomplished by rapidly alighting on the tips of the tarsi, flexing the legs slightly, and pushing off into flight once more, the wings vibrating all the while. As the fly thus bounces, at about 90 times per minute, it occasionally and quite suddenly thrusts the tip of the abdomen deeply into the moss, withdrawing it almost immediately. The fly may repeat this motion as many as 25 or 30 times before departing to another place.

The activity associated with oviposition in these three species was quite uniform, and it therefore seems that it may be rather similar in the other species, allowing of course for some modification due to differences in the kind of habitat, as for example whether the moss surfaces are vertical or horizontal. In the mosses, the eggs are found to be laid singly but several in a small area; that is, while several may be found within a space an inch in diameter, they do not occur in any sort of cluster, such as has been described for some other Tipulinae. In the laboratory, also, eggs are deposited singly, except when the available substrate is so limited as to force females to lay their eggs in groups.

EGGS

Matured eggs of all species of North American *Dolichopeza* have the same general appearance: oblong, slightly narrower at the posterior end, and with a chorion of intense black color, with a bluish or purplish, almost metallic sheen. The chorion is so smooth that at more than 200 × magnification there is no indication whatsoever of any surface sculpture. The position of the micropyle is indicated by an indentation of the chorion on the ventral surface, near the anterior end (Fig. 76). Orientation of the egg is based upon the usual position of the larva at the time of hatching.

Within the ovarioles, the developing eggs appear as buff colored, granular, oblong bodies. The smooth chorion is found only on those eggs which have moved into the lateral oviducts or are in the extreme lower ends of the ovarioles. Pale colored at the time of emergence of the adult female, the eggs soon darken, so that in a female only a few hours old the lateral oviducts are bulging with black masses of fully-formed eggs, all lying more or less horizontally, with their posterior ends directed towards the gonopore.

Eggs of some species of *Dolichopeza* bear a terminal filament of great length, the function of which seems to be retention of the egg in the moss where it is laid. This structure originates from a whitish cap of cells upon the end of the developing egg (Fig. 74) and by the time of oviposition has the form of a springlike, broadly conical, tight coil. Drawn out to its full length, it is seen to be from ten to fifteen times the length of the egg itself. I have not been able to correlate the presence or absence of the terminal filament with either the type of larval habitat or the phylogenetic affinities of the species. It is present in *Dolichopeza americana,* in *johnsonella, obscura* and *tridenticulata* of the *obscura* group, and in *sayi* of the *sayi* group. It is totally absent in *subalbipes* of the *obscura* group, and in *carolus, dorsalis, similis, subvenosa, venosa* and *walleyi* of the *sayi* group. Curiously, in all three races of *polita* it is present in a very rudimentary form, although recognizably different in each subspecies. In the typical subspecies (Fig. 77) the filament usually forms one open coil or loop; in the western subspecies it has the shape of a hook and never forms a complete coil; and in the central race it forms one or two irregular coils in a plane perpendicular to the basal part of the filament.

In attempting to find out what numbers of eggs are laid (or are probably laid) by the various species, I have dissected females that were collected into alcohol at a time when they seemed to be still rather teneral and quite filled with eggs, even into the first abdominal segment. In such females, it is difficult to imagine where more eggs would be placed if there were any more, so the count of matured and nearly matured eggs present was taken as the number which the fly would probably have oviposited. In nearly-spent females, perhaps only one or two matured eggs may be found in the oviducts, while the very much undeveloped eggs in the ovarioles are still in place. Thus, there seems not to be a continuing development of eggs throughout the period of oviposition, but rather a brief initial period of maturing of all those eggs which are going to be laid at all. Egg counts in females of several species from different parts of the country are surprisingly constant, varying in the vicinity of 100 to 140, depending on the species. Rogers (1933: 32) gives the number of eggs actually laid as 250 to 350 for the Tipulinae in general, and, in an unpublished paper, the numbers 200 and 250, more or less, for two individuals of *Dolichopeza obscura* from Florida. However, my examination of another Florida female of *obscura,* in which all eggs seemed to be still in place, revealed 104 eggs in advanced stages of maturity and no more than three dozen countable eggs in the ovarioles. A very teneral female *tridenticulata* from Jefferson County, Indiana, contained 90 fairly darkened eggs and about 50 in various developmental stages. From a female *americana,* 106 matured eggs were taken, and there were not many others that looked as if they might eventually have been laid. From all the indications available to me, I would estimate the potential egg production of an average female of *Dolichopeza* to be about 120 eggs.

Dimensions of the eggs vary somewhat proportionally with the body size of the individual female and only very generally with the average body size of the species. The smallest eggs measured were of the small species, *Dolichopeza americana* and *tridenticulata,* while the largest eggs found were those of *similis,* the largest *Dolichopeza.* Average dimensions of eggs from average sized females were:

americana—.60 x .25 mm.
carolus—.79 x .37 mm.
dorsalis—.76 x .31 mm.
johnsonella—.74 x .29 mm.
obscura—.73 x .40 mm.
polita ssp.—.75 x .30 mm.
sayi—.72 x .31 mm.
similis—.92 x .35 mm.
subalbipes—.83 x .36 mm.
subvenosa—.75 x .31 mm.
tridenticulata—.65 x .30 mm.
venosa—.79 x .32 mm.
walleyi—.76 x .32 mm.

Measurements were made with a camera lucida scale from eggs mounted on slides. Because the eggs are likely to be somewhat flattened when so mounted, the widths given here are subject to slight error.

Duration of the egg stage in *Dolichopeza* has been reported only once (Rogers, 1933: 32), the time given being 13 to 16 days, for *D. obscura* at outdoor temperatures in March and April, in Florida. However, among several groups of eggs kept at both room and outdoor temperatures, in Indiana, Michigan and Minnesota, I have found the time to be closer to eight days. My observations are summarized in Table 2.

TABLE 2.—Duration of the Egg Stage in Some Species of North American *Dolichopeza*

Species	Date of hatching	Duration of egg stage	Where kept
americana	19 Aug.	7-8 days	laboratory
carolus	24 June	9 days	outdoors (Indiana)
dorsalis	22 July	9 days	outdoors (Minnesota)
johnsonella	29 June	8-9 days	outdoors (Indiana)
obscura	2 Aug.?	10 days?	laboratory
polita ssp.	24 Aug.	7-8 days	laboratory
polita ssp.	6 Sept.	7-8 days	laboratory
sayi	6 Sept.	6-7 days	laboratory
sayi	26 Sept.	7 days	laboratory
similis	25 June	7 days	laboratory
venosa	8 June	7 days	laboratory
walleyi	9 June	7-8 days	laboratory

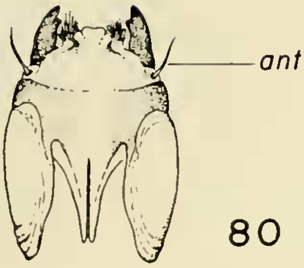
Durations are given from time of oviposition to date of abundant hatching. Where the length of the egg stage is indicated as uncertain, the date of oviposition of the first eggs to hatch is not known but is one of two known dates. It will be noted that outdoor times are in all cases the longer, except for *obscura*, which was in an unheated building in the woods of northern Michigan. Laboratory or room temperatures seem to accelerate development by about one day.

LARVAE—MORPHOLOGY

First instar larva.—As it comes from the egg, the larva of *Dolichopeza* seems to be mostly head capsule and caudal setae (Fig. 78); the body is extremely short and transparent, and only the tips of the mandibles are at all strongly sclerotized. Within three or four hours after hatching, however, the larva stretches out to somewhat less than two millimeters in length, exclusive of the caudal setae, and the head capsule, darkened to a grayish color, becomes discernible in some detail. At first nearly rectangular in outline when seen from above, the head assumes its more oval shape in about a day. The integument of the very young larva becomes a dirty yellowish color, yet is transparent enough that the viscera show clearly through it; and it bears an inconspicuous covering of extremely minute hairs, in addition to the weak bristles indicated in Figure 79.

There are several details in which the head of the first instar larva (Fig. 80) differs markedly from that of later instars. Perhaps the most conspicuous of these is the antennal structure. In later instars, the antennae are cylindrical, with an apical sensory peg, but in the first instar they are setiform. The fronto-clypeal plate is relatively larger, and the backward extensions of the lateral plates that parallel it in later instars are absent in the very young larva. Although not studied in more than a few species, the mandibles, mentum and hypopharynx generally have fewer and more rounded teeth than their counterparts in the more mature larva. In the heavily sclerotized head capsules of older larvae, I had long overlooked the eyes, but their position in the first instar larva is clearly indicated by concentrated spots of violet-purple pigment similar in color to that associated with the compound eyes of the adult flies.

The spiracular disc of the first instar larva contrasts even more remarkably with those of all subsequent instars; in fact, except for the presence of spiracles, it has almost no characteristics in common with them. Below the spiracular openings are four sclerotized



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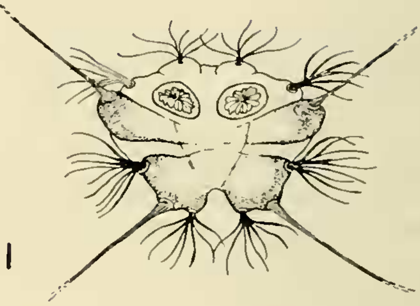

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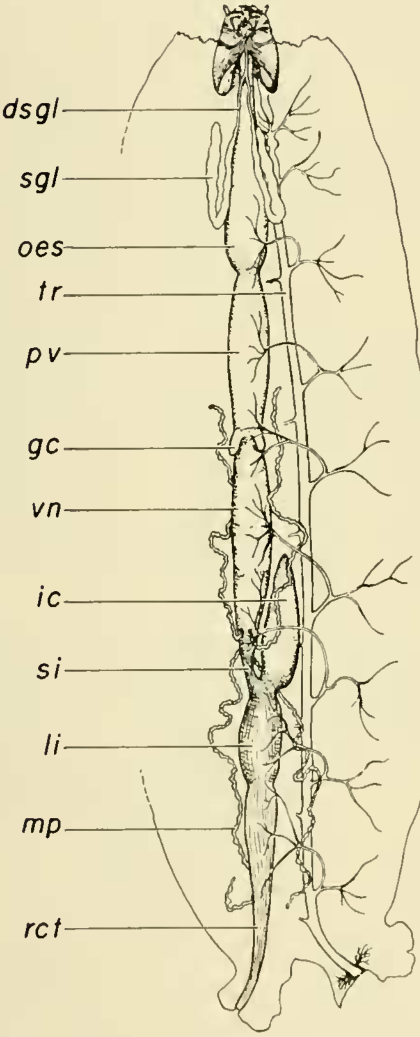

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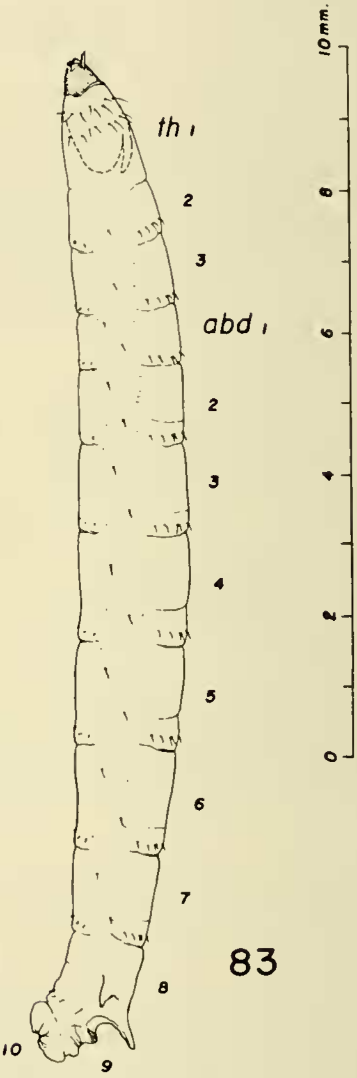

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FIG. 80. Head capsule of first instar larva of *Dolichopeza (Oropeza)* sp.; ant—antenna. FIG. 81. Spiracular disc and associated structures of first instar larva of *Dolichopeza (Oropeza) obscura.* FIG. 82. Gross internal anatomy, digestive and respiratory systems only, of fourth instar larva of *Dolichopeza (Oropeza) obscura;* dsgl—duct of salivary gland, gc—gastric caecum, ic—intestinal caecum, li—large intestine, mp—Malpighian tubule, oes—oesophagus, pv—proventriculus, rct—rectum, sgl—salivary gland, si—small intestine, tr—trachea, vn—ventriculus. FIG. 83. Fourth instar larva of *Dolichopeza (Oropeza) obscura,* indicating thoracic and abdominal segmentation; th—thorax, abd—abdomen.

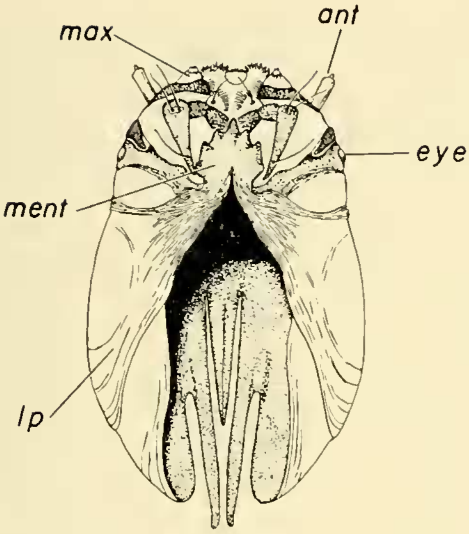
plates, a dorsal pair narrowly fused at the midline and a ventral pair of broader plates, the medial borders of which are indistinct. Each of these plates bears a long, slender caudal seta on its distal margin (Figs. 79 and 81). Across the top of the spiracular disc are four broadly-rounded, low protuberances, each with a tuft of bristles at its apex. Two similar tufts of bristles are borne on each of the ventral plates, in the positions shown in Figure 81. It is difficult to homologize these various structures with those seen on the spiracular disc of the older larva. However, it seems not unlikely that the four dorsal protuberances correspond to the four conical dorsal lobes found in the same position in the later instars. Either pair of sclerotized plates may be homologous with sclerotized, bristle-bearing areas of relatively much smaller extent on the ventral lobes of the spiracular disc of the more mature larva; but I am more inclined to believe that it is the lower pair, which means the upper pair has no counterpart in the older larva. The general similarity of the spiracular disc of the very young *Dolichopeza* larva to that of the later stage larvae of some Limoniinae (such as *Limnophila* and *Pseudolimnophila*) is striking. The very long caudal setae and tufts of bristles possibly serve to hold the respiratory openings above the water surface in case the larval habitat becomes saturated. Similar structures are found in the first instar as well as later stage larvae of the more aquatic relatives of *Dolichopeza,* such as *Megistocera* (Rogers, 1949:9); therefore, it may be that these bristles and setae have no function in *Dolichopeza* but are merely rudiments inherited from ancestors that lived in wetter habitats. I have observed that some larvae lose part or all of one or more caudal setae and apparently are none the worse for it. With the first molt, the tufts of bristles and the sclerotized plates and their setae are all lost.

Fourth instar larva.—Larvae in the second, third and fourth instars differ mostly in size and are so similar in structure that a description of the last will suffice for all. The body is elongate, nearly terete but slightly depressed, thickest at mid-length, tapering rather evenly and gradually toward both ends, 12 to 18 millimeters in length and about two millimeters in breadth, depending on the species. The skin is thin and soft but tough. It is covered by extremely small patches and rows of microscopic hairs, variously arranged according to the species. In most species, there are also transverse ridges of larger hairs on both the dorsal and ventral surfaces but more distinctly developed on the dorsum.

The body of the larva consists of a strongly sclerotized, oval, depressed head capsule, three "thoracic" segments and ten "abdominal" segments, of which all are rather easily distinguishable except the last two (Fig. 83). Heretofore, the region I have designated the ninth and tenth abdominal segments has been considered a single segment (Wardle, 1926:29) but may comprise the ninth through eleventh morphological segments, while that which I have indicated as the prothorax has been regarded as two segments, probably because it bears two rows of bristles instead of the single row found on most other segments. The interpretation of segmentation presented here is based upon studies of the internal as well as external anatomy of the larva and upon correlation of larval structures with those of the pupal and adult stages.

Head and mouthparts.—Since virtually the only larval structures that are strongly sclerotized, hence of fixed size and shape, are associated with the head, this part of the larva has been studied in considerable detail by earlier investigators. Thus, Alexander (1920:983) gives a rather detailed descriptive paragraph on the head and mouthparts of the larva of *Dolichopeza tridenticulata* (as *Oropeza obscura*), the only North American species concerning which there are any published morphological data. The head has the characteristic tipuline appearance. Its sides are formed by the large lateral plates, which by their oval outline, striated pattern and concavo-convex shape somewhat suggest deep clam shells. Cook (1949:8) regarded these lateral plates as belonging to the maxillary segment of the head, in *Holorusia,* but I cannot accept such an interpretation in the case of *Dolichopeza.* That the muscles of the mandibles and maxillae originate on the lateral plates suggests rather that these plates are homologous with the vertex of the ocular segment, as in so many other kinds of larvae.

Ventrally, the lateral plates are separated by a somewhat triangular space (Fig. 84), but dorsally they fuse with the narrowly triangular fronto-clypeus (Fig. 85, fclp) along much of its length. From the dorsal margin of each lateral plate, a bladelike projection extends backward alongside the frontoclypeus, slightly exceeding the posterior end of the lateral plate in species of *Oropeza* but conspicuously longer in the subgenus *Dolichopeza.* The sclerite I have designated as the fronto-clypeus has been called the epicranial plate by Comstock and Kellogg (1902) and the clypeus by Cook (1949), who so identified it by the fact that the muscles of the cibarium originate on it. However, the dorsal muscles of the



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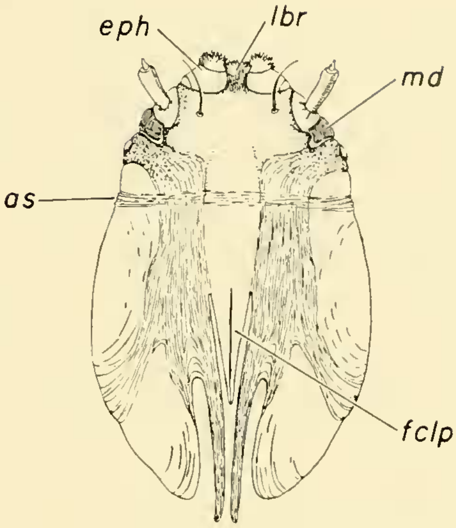

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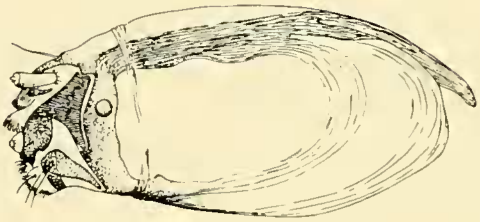

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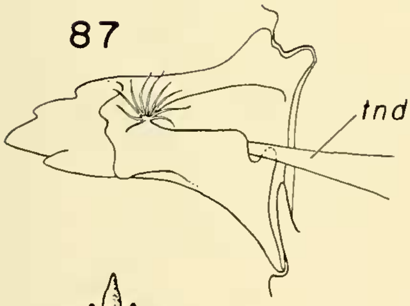

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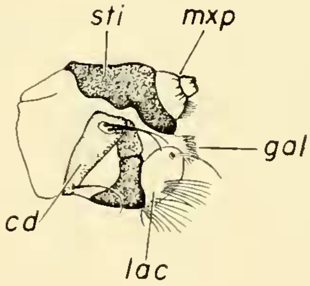

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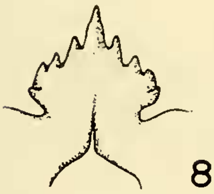

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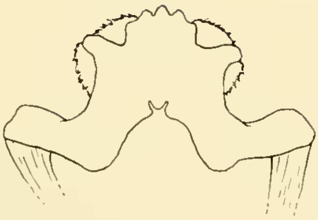

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FIG. 84. Head capsule of fourth instar larva of *Dolichopeza (Oropeza) obscura,* ventral aspect; ant—antenna, lp—lateral plate, max—maxilla, ment—mentum. FIG. 85. Same as 84, dorsal aspect; as—line of attachment of skin, eph—epipharynx, fclp—fronto-clypeus, lbr—labrum, md—mandible. FIG. 86. Same as 84, left lateral aspect. FIG. 87. Right mandible of fourth instar larva of *Dolichopeza (Oropeza) similis,* mesial aspect; tnd—tendon of adductor muscles of mandible. FIG. 88. Right maxilla of fourth instar larva of *Dolichopeza (Oropeza) obscura,* ventrolateral aspect; cd—cardo, gal—galea, lac—lacinia, mxp—maxillary palp, sti—stipes. FIG. 89. Mentum of *Dolichopeza (Oropeza) similis,* ventral aspect. FIG. 90. Hypopharynx of *Dolichopeza (Oropeza) dorsalis,* ventral aspect.

pharynx, which typically have their origin on the front, also originate on this same sclerite, which is why I regard it as the fronto-clypeus. A zone of fine wrinkles girdles the entire head at the line of attachment of the skin. The fronto-clypeus joins the labrum almost imperceptibly. A large bristle, subequal in length to the antenna, is borne near the middle of each side of the labrum, and a narrow, medial projection from the anterior margin of the labrum appears to bisect the broad, brushy epipharynx, to which it is immovably joined. The antennae consist of a cylindrical basal segment about four times as long as thick and an apical sensory peg. They are attached to membranous areas at either side of the labrum. Below the labrum-epipharynx are the mandibles, each of which articulates on a blunt dorsal condyle at the junction of the lateral edge of the labrum with the lateral plate and an elongate ventral one on the mid-anterior edge of the lateral plate (Figs. 86, 87). The mandible has four marginal teeth (rarely five) and a broad, inner molar protuberance having somewhat the form of a ridge across the mandible. Behind this molar ridge is an excavation within which is attached the tendon of the adductor muscle of the mandible and at the distal end of which is situated a small tuft of bristles. This tuft has been called the brustia; its function is unknown to me. Attached below the mandibles but overlapping them apically are the subrectangular maxillae. The maxilla (Fig. 88) comprises a narrowly triangular cardo bearing three long setae, an irregularly shaped and very heavily sclerotized stipes, a blunt maxillary palp, and the indistinctly differentiated, apically hairy galea and lacinia, the latter more ventral in position. The mouth cavity is closed ventrally by the mentum, a structure formed by the fusion of forward extensions of the lateral plates (Fig. 84). In some species, particularly in the *obscura* group, the mentum usually has only five rather blunt teeth, but in others (as *D. similis*, Fig. 89) they number seven and are more acute. In all species, there is in addition a small lateral tubercle at each side of the base of the mentum. Just dorsal to the mentum, within the mouth cavity, is the hypopharynx, into which the salivary duct empties. Its upper part is weakly sclerotized and covered with hairs, but the lower portion is strongly sclerotized and bears usually three blunt teeth (Fig. 90). The shapes of the hypopharynx and mentum, specifically of their toothed margins, have been found of limited use in the recognition of species.

Since larvae of *Dolichopeza* are sensitive to light, it seems only reasonable to suspect that they have eyes of some sort, which they do. The eyes consist externally of a single, circular, only slightly protruding ocellus. They are situated one at either side of the head, in the foremost part of the lateral plate, just behind the mandible (Fig. 86). As the pigmented portion of the eye behind the hyaline lens is dark, the eyes are well concealed in the densely sclerotized walls of the head. Probably all crane fly larvae have eyes, but references to their existence in the larvae of the subfamily Tipulinae are rare. Peterson (1951: 256) probably was referring to species of the Limoniinae when he wrote "ocelli . . . may occur adjacent to the mandibles." At any rate, his figure C, page 279, shows no eyes in *Tipula abdominalis*. Cook (1949), in a detailed study of the head capsule of *Holorusia rubiginosa*, noted the presence of eyes in that species; but most authors, less attentive to detail, have generally overlooked them throughout the Tipulinae, Comstock and Kellogg having failed to observe them even in *Holorusia rubiginosa*, a species they described in detail. In the less strongly sclerotized head capsules of some Limoniinae, such as *Pedicia* and *Dicranota*, the eyes are more easily seen but still have been referred to only cautiously as "eye spots" (Miall, 1893: 237 and plate I; Alexander, 1920: 1092, plate LXI).

Caudal segments.—On comparing genera of larval crane flies, one's attention is almost invariably drawn first to the spiracular disc, which is the area surrounding the two large spiracles on the ninth abdominal segment. This ordinarily well-exposed surface usually exhibits great differences from genus to genus and often easily noticeable differences among species within a large genus. Within groups of closely related species such as North American *Dolichopeza*, however, there is considerable uniformity in the appearance of the spiracular disc and its surrounding structures. In larvae of *Dolichopeza*, the spiracular disc is generally devoid of hairs but has three pairs of small, darkly sclerotized plates disposed around the spiracles as shown in Figure 92. Just below the disc are two broad, rounded lobes, each having a sclerotized apex from which extends a weak bristle. Other bristles occur on the sides of these lobes as shown. Above the disc are the more or less conical, fleshy lobes to which reference has already been made in the discussion of the first instar larva. These four lobes are, in one form or another, characteristic of all species of Tipulinae, although the belief that there were only three dorsal lobes in *Dolichopeza* s. s., as first described by Beling (1886: 190), has persisted almost to the present day (for example, see Hennig, 1950: 396). Beling stated that, of the usual four lobes above the spiracular disc in larval tipulines, the middle two in *Dolichopeza albipes* of Europe are grown together. Since Beling's time, several authors have commented on this condition, it being unique among all Tipulinae. When I first found the larva of *Dolichopeza americana,* in the winter of 1949, I noted that the apparently single median lobe was actually formed of two lobes closely appressed and that the two separated easily at the light touch of a needle. It seemed that the same might be true of *D. albipes,* but it was not until 1955 that I was able to verify this by examination of specimens in the British Museum. Only once among several hundred larvae examined have I found an instance of true complete fusion of the middle lobes. This was in a fourth instar larva of *D. sayi,* which in the third instar had been quite normal (see Fig. 39). This unusual specimen was preserved because of its singularity.

Situated dorsolaterally on each side of the eighth abdominal segment of larvae of the subgenus *Oropeza* is a subconical lobe (Fig. 92), similar in texture and often in size to the outer lobes above the spiracular disc. These lobes are characteristic of *Oropeza* but are also found in at least one other subgenus, *Trichodolichopeza,* or at least in the only two species, *hirtipennis* and *flavifrons* of South Africa, known in the larval stage (Wood, 1952: 88). Absence of such lobes on the sides of the eighth abdominal segment in the subgenus *Dolichopeza* (Fig. 91) gives those larvae somewhat the appearance of larvae of *Tipula,* but the green color and peculiar markings of the dorsum (Fig. 97) are different from any *Tipula* known to me and should make differentiation easy.

The tenth abdominal segment, or anal segment, is located ventrally with respect to the ninth and comprises four blunt, pale, membranous lobes surrounding the anus. There is no doubt that these lobes are homologous with the anal gills developed in many species of Tipulinae as well as rather generally in the family; however, as they appear on dissection to have no respiratory function (as discussed below), I shall refer to them merely as anal lobes. There are a supra-anal or posterior pair and a sub-anal pair.

Integument.—The soft but tough larval skin bears two size categories of microscopic hairs, in addition to the macroscopic setae (which are the same in all species). As the hair patterns of the dorsum and venter are in general similar, although much less well developed on the underside of the body, a description applying in detail only to the dorsum follows. Seen by the unaided eye or only slightly magnified, the larva of *Dolichopeza* appears to have many darkened, transverse ridges on its back. In some species, these occur six or seven (rarely eight) per body segment, except where they are obscurely merged on the thorax and on the eighth abdominal segment; but in other species it is difficult to discern separate ridges at all, due to their irregular distribution. Using magnifications near 30 or 40 ×, the transverse ridges are seen to be formed of rows of hairs (Fig. 94). These, the larger of the two sizes of microscopic hairs, are many times as long as they are in diameter. The other size referred to are extremely short and appear to be no more than tiny spots, except at very high magnifications. At medium magnifications, rows of these minute hairs look like short, dark lines in the areas between transverse ridges and oriented more or less parallel to the ridges; but at high magnifications (60 to 80 ×) they may be seen as individual, short hairs, arranged in short or long rows (Figs. 95, 96). On the pleura the minute hairs may be arranged in rather circular patches or may occur singly, while the longer hairs are absent. As the pattern of distribution of these two kinds of integumental hairs seems to be fairly constant for a species, I have made extensive use of it in the key that follows this section.

Internal anatomy.—The internal structure of larvae of *Dolichopeza* was examined only in a general way, in an attempt to find specific or group characters for taxonomic use, but the anatomy of all species studied was found to be rather uniform. Only the digestive, tracheal and nervous systems are discussed here. The sketch of the internal organs (Fig. 82) was made from a larva killed by immersion in boiling water, which accounts for the outstretched condition of all the viscera. In living larvae or those killed by means other than heat, the organs are shorter, broader and not so linearly arranged. The body cavity, especially posteriorly from about mid-length of the ventriculus, is largely occupied by a whitish or light gray perforated sheet of adipose tissue.

Digestive system.—Most conspicuous of the internal structures are the organs of the digestive tract. The oesophagus is a muscular tube, often enlarged at its posterior end. At either side of it lie the whitish-hyaline salivary glands, shown in Figure 82 with a single curve at about their mid-length, although they sometimes are doubly convoluted. Each salivary gland has a narrow lumen surrounded by a secretory portion made up of a single layer of large, cuboidal cells which have correspondingly large central nuclei containing long and much intertwined chromosomes. The chromosomes were not examined in detail. The salivary glands are partially invested with adipose tissue, especially apically, and are drained by slender salivary ducts which unite beneath the oesophagus just within the head capsule. Separated from the oesophagus by a slight constriction is the proventriculus, which in turn empties into the thick-walled, muscular ventriculus. Two short, glistening, pocket-like gastric caeca are appended to each side of the anterior end of the ventriculus, and its posterior end is marked by the attachment of four Malpighian tubules, beaded in appearance except for their nearly-transparent proximal ends, and similarly arranged two at each side of the ventriculus. A short, slender small intestine connects the ventriculus with the sac-like anterior end of the large intestine, to which is also joined a large, thick-walled diverticulum, the intestinal caecum. This caecum is always found, in freshly killed larvae, to be filled with particles of food and countless bacilliform bacteria which are probably symbiotically related to the larva. The large intestine tapers toward the rectum, the junction between these two regions being poorly defined. A comparison of the relatively simple digestive system of a carnivorous tipulid larva such as *Dicranota* (Miall, 1893) with that of moss-eating *Dolichopeza,* with its voluminous divisions and many caeca, recalls similar differences between carnivorous and herbivorous mammals.

Tracheal system.—Two main tracheal trunks extend from the spiracles on the ninth abdominal segment to the anterior part of the mesothorax. They are situated close beneath the dorsolateral body wall, through which they may readily be seen in living larvae. From a bulb-like thickening at the mesothoracic terminus of each trunk, seven branch tracheae are given off to the brain, various parts of the inside of the head, and to the body wall of the prothorax and mesothorax. A metathoracic branch at about mid-length in that segment appears to supply oxygen to the adjacent body wall only. In each abdominal segment from the first through the seventh, there is a pair of ventrolateral tracheal branches, each dividing in turn into a short branch to the muscles and skin of the body wall and a longer visceral branch (Fig. 82); and in each segment there is a slender tracheal connection between the two trunks, passing near the dorsal vessel and probably oxygenating it. Only the bases of these dorsal commissures are indicated in the sketch. The visceral tracheae are longest in the mid-region of the body, where maximum displacement occurs, during locomotion, between the digestive organs and the relatively stationary tracheal trunks. The point of branching from the trunk and the general visceral destination of the abdominal tracheal branches of one side are summarized as follows:

First abdominal branch: from posterior part of first segment or anterior part of second; to posterior oesophagus and anterior proventriculus.

Second branch: from anterior part of third segment; to proventriculus.

Third branch: from anterior part of fourth segment; to proventriculus and ventriculus in region of caeca.

Fourth branch: from near junction of fourth and fifth segments; to ventriculus.

Fifth branch: from posterior part of fifth segment; to small intestine and posterior part of ventriculus.

Sixth branch: from posterior part of sixth segment; to large intestine.

Seventh branch: from mid-region of seventh segment; to rectum.

The eighth and ninth abdominal segments have no dorsal commissures or visceral branches but are oxygenated by short, much branched tracheae given off just anterior to the spiracle. A few branches from this same source reach the anal lobes, but the tracheation of these is so slight that it seems unlikely that they could serve a respiratory function.

Central nervous system.—As in other crane fly larvae, the brain of *Dolichopeza* is located in the prothorax, outside the head capsule. It is composed of two subspherical lobes, narrowly joined and giving off three anterior branches, which I have not traced but which are presumed to innervate the eyes, antennae and labrum (see Cook, 1949: 39). The brain lies just below and before the open anterior end of the dorsal vessel, or aorta. Circumoesophageal commissures connect the brain with the suboesophageal ganglion, from the anterior surface of which arise two large nerves, each of which divides into three branches innervating certain mouthparts. From the posterior surface of the suboesophageal ganglion, two stout nerve cords converge to connect with the first of a series of four large, rounded and depressed ganglia lying against the floor of the mesothorax and anteriormost metathorax. The first three of these large ganglia supposedly belong to the three thoracic segments, while the last possibly represents the fusion of two or more abdominal ganglia. Ganglia of somewhat smaller size occur in the posterior part of the first abdominal segment, anterior part of the third, near the middle of the fourth, fifth and sixth, and in the anterior half of the seventh abdominal segments. Some tipulid larvae have one or two additional ganglia, but the equivalents of these in the larva of *Dolichopeza* are unknown. Behind the last ganglion, the two main strands of the ventral nerve cord diverge and bend posterodorsally, giving off several branches. None of the branches of the central nervous system was traced in detail.

Larval key characters.—As stated earlier, most keys to crane fly larvae have made use of characters of the spiracular disc and the head, particularly the mouthparts. Among species of *Dolichopeza,* however, there is such similarity of apperance of the spiracular disc and the lobes surrounding it that I have so far been able to make only limited use of these structures in species recognition; and to utilize details of the head capsule in taxonomy almost always requires dissection of the larva. For life history studies or other reasons, it is often desirable to segregate larvae before preservation. Accordingly, taxonomic characters were sought that would allow species identification of living larvae. A satisfactory means of species separation has been found in the pattern of distribution of the two sizes of microscopic hairs of the integument discussed earlier in this section, used in conjunction with the few reliably consistent differences in the caudal segments.

The key that follows has certain limitations. Mature larvae of *Dolichopeza carolus, johnsonella, subvenosa* and two new species described herein are still unknown; and I have reared certain of the other species only a few times and from only a very few localities within their total ranges. The key, however, is reliable to the extent of the material examined. Comments on the species as yet unknown will be found under the respective species headings in the systematic account.

Although prepared on the basis of fourth instar larvae, this key may prove adequate for second and third instar larvae as well. Magnifications of 30 to 80 × have been used in describing characters, but some observations have been verified by use of the compound microscope.

TENTATIVE KEY TO FOURTH INSTAR LARVAE OF NORTH AMERICAN *DOLICHOPEZA*

1. Body coloration in life green with two series of irregular brown to black spots on dorsum (Fig. 97); median lobes above spiracular disc closely appressed; no conical projections from dorsolateral surfaces of eighth abdominal segment (Fig. 91) (subgenus *Dolichopeza*) . . . . *americana*

   Body coloration in life greenish, brownish or some blending of these, lacking spots or other markings, except for transverse ridges of small

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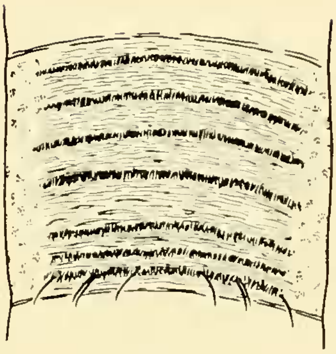

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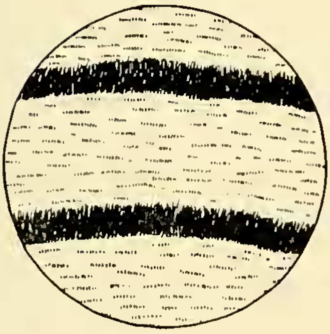

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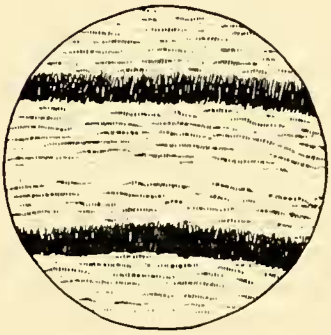

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FIG. 91. Cauda of larva of *Dolichopeza (Dolichopeza) americana*. FIG. 92. Cauda of larva of *Dolichopeza (Oropeza) obscura*. FIG. 93. Typical abdominal segment of fourth instar larva of *Dolichopeza (Oropeza) subalbipes*, dorsal aspect. FIG. 94. Same as 93, *Dolichopeza (Oropeza) obscura*. FIG. 95. Detail of dorsum of fourth instar larva of *Dolichopeza (Oropeza) walleyi*. FIG. 96. Same as 95, *Dolichopeza (Oropeza) sayi*.

hairs; median lobes above spiracular disc distinctly separated; a conical or subconical projection from each dorsolateral surface of eighth abdominal segment (Fig. 92) (subgenus *Oropeza*) 2

2. Minute microscopic hairs of pleura single, thickened and peg-like; those of dorsum sometimes in rows of various lengths but also often occurring singly; transverse ridges of larger microscopic hairs rarely indicated, never dense 3

   Minute microscopic hairs of pleura grouped in small, circular patches, the individual hairs not thickened and not seen as separate hairs except at high magnifications; those of dorsum arranged in transverse rows or very rarely single; transverse ridges of larger microscopic hairs evident on most body segments but may be weak on second through sixth abdominal segments 4

3. Minute microscopic hairs of pleura of eighth abdominal segment as numerous, dense or evenly distributed as those of seventh and other segments .... *polita* sspp.

   Minute microscopic hairs of pleura of eighth abdominal segment sparse or irregularly distributed, leaving bare areas .... *tridenticulata*

4. Larger microscopic hairs of dorsum arranged in dense transverse ridges that are variously interrupted, deflected or staggered (Fig. 93), so that it is difficult to count the number of ridges on a typical abdominal segment 5

   Larger microscopic hairs of dorsum arranged in subparallel transverse ridges, usually numbering six or seven per segment (Fig. 94); ridges may be weak on abdominal segments two through six 6

5. Minute microscopic hairs in short rows of varying lengths, the rows distinct, clearly separated .... *venosa*

   Minute microscopic hairs in long, indefinite rows with poorly defined terminations, or not clearly arranged in rows (Fig. 93) .... *subalbipes*

6. Minute microscopic hairs in short, distinct rows with clearly defined terminations, the rows clearly separated (Fig. 95) 7

   Minute microscopic hairs in long, indefinite rows with poorly defined terminations, or not clearly arranged in rows (Fig. 96) 8

7. Dorsolateral lobes of eighth abdominal segment nearly conical, of about same shape as lateral lobes above spiracular disc and approximately two-thirds as long as the latter .... *walleyi*

   Dorsolateral lobes of eighth abdominal segment short and blunt, only half or less than half as long as lateral lobes above spiracular disc .... *similis*

8. Transverse ridges of larger microscopic hairs about equally well marked on all abdominal segments .... *obscura*

   Transverse ridges of larger microscopic hairs more weakly developed on second through fifth (or sixth) abdominal segments than on thoracic, first and seventh abdominal segments 9

9. Minute microscopic hairs clearly in rows, the rows crowded together near transverse ridges of larger microscopic hairs, leaving a narrow zone without hairs (Fig. 96) .... *sayi*

   Minute microscopic hairs usually in poorly defined rows, the rows about evenly distributed between transverse ridges of larger microscopic hairs; hairs long and dense on eighth abdominal segment ...... *dorsalis*

LARVAE—NATURAL HISTORY

It is in the larval state that an individual of *Dolichopeza* passes most of its existence, from only a few days after the egg is laid until about a week before the adult is on the wing. In regions where there are two annual generations, this span of time may be about 280 days in the overwintering generation but only about 50 days in the summer generation (Fig. 99). Larval life comprises four stadia, the last much the longest in duration.

Eggs about to hatch pulsate slightly and irregularly for as much

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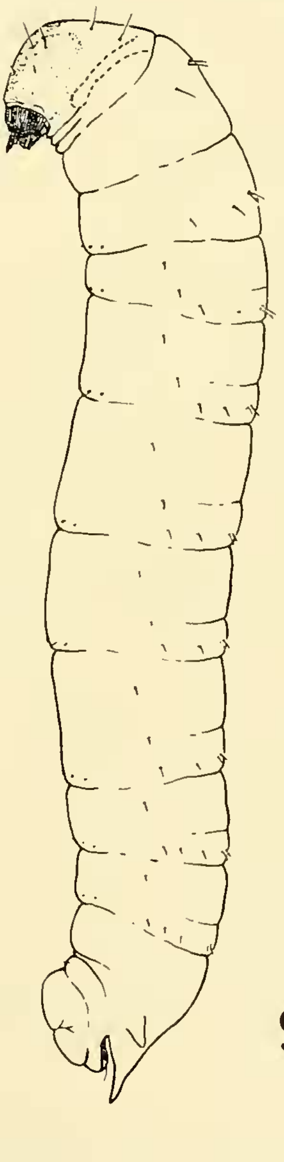

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FIG. 97. Fourth instar larva of *Dolichopeza (Dolichopeza) americana,* dorsal aspect. FIG. 98. Fourth instar larva of *Dolichopeza (Oropeza) obscura* just before emergence of the pupa; note position of head capsule, pupal thoracic respiratory horn visible through larval skin, and contracted lobes of spiracular disc.

as three hours before the chorion ruptures. At hatching, the chorion splits nearly the full length of the egg, mostly along the dorsal side but somewhat on the ventral side, and the head of the young larva appears, mandibles foremost. Grasping at plant fragments or other surrounding objects with its jaws, the larva pulls itself free of the egg covering in a few minutes. Within a few hours the relative proportions of the body of the larva change markedly, as described in the preceding section and illustrated in Figures 78 and 79. Once freed from the egg, the larva sets out almost immediately in search of food, clamping its mandibles firmly into whatever it encounters.* For this reason, newly-hatched larvae in the laboratory must be provided with food, if several are kept together, or they will commence biting each other.

Very young larvae are extremely sensitive to instabilities of environment, such as abrupt changes in temperature or moisture. As mentioned earlier, they drown readily in small excesses of moisture. They perish equally rapidly when subjected to even slight desiccation. Mortality of first instar larvae in the laboratory was very high in all species, possibly because no special equipment was employed to stabilize either humidity or temperature.

Although young larvae appear able by the remarkable gape of their jaws to partake of parts of moss leaves such as are eaten by more mature larvae, their earliest diet seems to consist primarily of material scraped from leaf surfaces and plant scraps which collect about moss stems. Within a day of their emergence, they have gorged themselves so that the alimentary canal may be clearly seen as a bright green streak from one end to the other of the nearly transparent body. Confined to small dishes in the laboratory, very young larvae frequently devoured others that had died, and somehow opened and consumed the contents of unhatched, presumably unfertilized eggs, discarding the chorion. I do not take it from this that cannibalism is the rule in *Dolichopeza* but merely assume that available sources of protein are utilized whenever they are found by young larvae, just as they are by older larvae, which have been observed to feed on dead pupae and larvae in laboratory rearing dishes.

Duration of the first stadium is not constant, even among larvae of the same brood hatched about the same time. It usually varied from eight to fifteen days, indoors, although a few laggard individ-

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* This tactile response of the mandibles is a convenience in picking up the tiny larvae, which might be damaged by other means. A hair or bristle of a brush placed before the larva is soon seized between the jaws, and in the time it takes the larva to discover it has not got hold of food, it may be transferred to the desired place.

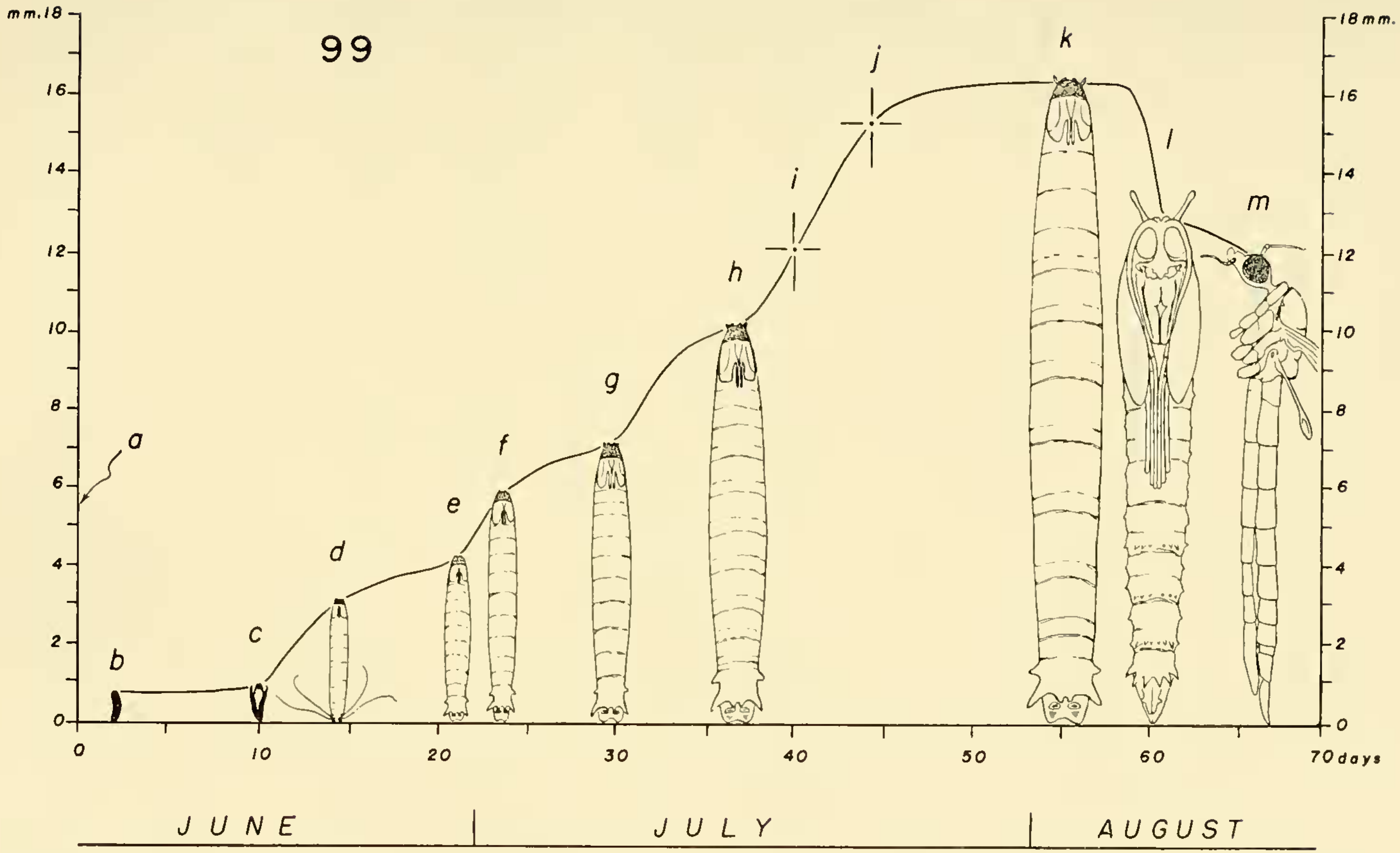

FIG. 99. Life cycle and growth in the summer generation of *Dolichopeza (Oropeza) sayi* in southern Michigan; a—time of oviposition, b—egg, c—hatching of egg, d—first instar larva, e-f—second instar larva, g—third instar larva, h—early fourth instar larva, i-j—growth indicators, fourth instar larva, k—late fourth instar larva, l—pupa, m—adult female.

uals required three weeks to pass to the next instar. Larvae reach a length of about four millimeters before the first ecdysis. Size change at molting is not noticeable, but some remarkable changes take place in the appearance of the larva. The four long caudal setae as well as the tufts of bristles (Fig. 81) are shed with the first larval skin. These structures are characteristic of the first instar larva of all species in which this instar was observed (*americana, carolus, dorsalis, johnsonella, obscura, polita* sspp., *sayi, similis, venosa* and *walleyi*); accordingly, their absence is taken as evidence that the first molt has occurred.

In the second instar, the larva of *Dolichopeza* resembles the later instars in general appearance. Although low and broad, the characteristic six lobes surrounding the spiracular disc are present and plainly visible, as are also the dorsolateral lobes of the eighth abdominal segment. At the first molt the larva also acquires the coating of microscopic hairs that gives the body the roughened surface so useful in locomotion. (There are hairs on the skin of the first instar larva, but they are so short and slender as to be scarcely visible at 200 × magnification.) Following the first ecdysis, the larva feeds more actively and grows rapidly, reaching the end of the second stadium in about five or six days.

Third and fourth instar larvae are almost identical in appearance, differing only in size. The third stadium may be as short as five days, so that some larvae may attain the fourth instar only about three weeks after hatching from the egg. Thus, the fourth stadium lasts as long as the other three combined, in the summer generation, and is much longer in the overwintering generation. Size increase is especially rapid during the first few days following a molt, in all instars (Fig. 99), and thereafter it proceeds more slowly. An explanation for this may be found in the fact that the larva ceases to eat for a short time preceding ecdysis, but once the mouthparts regain their strength and rigidity after the molt it commences to eat voraciously. Of those larvae that survived, in a rearing dish of *Dolichopeza sayi,* all that hatched on or about 26 September reached the fourth instar between 15 October and 5 November, indoors. This was in southern Michigan, where sunny days are common enough into late October that most larvae produced from late summer matings are able to attain the fourth, or at least the late third, instar before cold weather forces cessation of feeding and the winter quiescence.

Molting.—Several hours before shedding its skin, the larva of *Dolichopeza* ceases feeding and other activities, and the body slowly becomes turgid, assuming a swollen appearance like that sometimes seen in larvae that have been dead several hours. The caudal lobes become tumid and blunt, losing their nearly-conical shape, and the spiracular disc bulges outward. The head is fully extended, while the thorax close behind it is swollen with the skin darkened, almost black. In this inactive condition, the larva rests until the separation of old cuticle from new has been completed. When movement is resumed, shortly before the actual molt begins, a perfect duplication of bristles, microscopic hairs and all other external features of the larva may be seen through the old integument. The larva suddenly begins to jerk the anterior one-third or one-half of its body from side to side in frantic and spasmodic motions, the head capsule being bent further and further ventrad all the while. About two minutes after the onset of this activity, the skin splits along the dorsal mid-line of the thorax, just behind the old head capsule, and the head of the larva is thrust out. Only another sixty seconds or so are required for the virtual completion of sloughing off the old skin, as the pale and feeble larva crawls among the moss stems, working the old skin off by repeated body undulations and by scraping against its surroundings. Attached at the spiracular disc by the linings of the tracheal trunks, the crumpled molted skin is dragged about for a while and is nearly turned inside out before the tracheal linings pull out and the larva is at last free of its old skin. Each ecdysis seems to produce a double crisis in the life of the larva, first in the struggle to throw off the old skin and second in surviving the periods of comparative helplessness before and after the molt. In fact, I find it somewhat fatiguing merely to observe the process!

Each of the four larval instars of a given species may be recognized by the dimensions of the head capsule, which changes size abruptly at molting while the softer parts of the body increase gradually and continuously. Increase in breadth of the larval head by a more or less fixed factor at each ecdysis has been observed in many kinds of insects and has been summarized as Dyar's law. In *Dolichopeza (O.) sayi*, this fixed factor of increase was found to be 1.5. Thus, from the head capsule width of the first instar larva measured as 0.25 mm., one estimates 0.38 mm. as the width of the second, 0.57 mm. for the third, and 0.86 mm. for the fourth instar head capsule. Observed widths were 0.25 mm., 0.40

mm., 0.60 mm. and 0.85 mm., respectively, measured by means of a camera lucida scale. Head capsule length in this same series of specimens averaged 0.40 mm., 0.65 mm., 1.00 mm. and 1.50 mm. for the four larval instars, showing that length increase is not exactly proportional to width increase. In a single instance, a larva seemed, on the basis of the size of head capsule recovered from the pupal burrow, to have pupated at the end of the third stadium. No indication of a fifth instar was ever found.

Feeding.—Very young *Dolichopeza* larvae are able to obtain food by scraping the surfaces of moss leaves and may also eat organic debris of various sorts, including their own dead. From the fact that often only the head capsule could be recovered from a rearing dish soon after a larva had molted and that I once found a larva with its head directed toward its freshly-cast skin, I suspect that the larva may often eat its recent skin for its first meal following ecdysis. By far the greatest item in the diet of the second, third and fourth instar larvae, however, is leaves of certain mosses and leafy liverworts. The particular species of such food plants are listed later in this section, under ecological distribution.

Most feeding is done at or near the surface of the moss habitat, where the leaves are green and fresh. When isolated bits of moss are offered to larvae in rearing dishes, the leaves are largely or entirely consumed, while the stems and other parts are ordinarily rejected.

There is an interesting difference in feeding behavior between larvae of *Dolichopeza americana* and those of species of subgenus *Oropeza*. Larvae of all species of *Oropeza* are rather uniformly colored, brownish, greenish or some subtle blending of these (the color in any case largely dependent upon recent diet) and in general lack any pattern. Transverse ridges of microscopic hairs might be regarded as a pattern, but this is not of the obliterative sort that draws attention away from the shape of the insect. Therefore, *Oropeza* larvae are conspicuous against the background of greenish highlights and dark shadows characteristic of most mossy surfaces on which they feed. *Dolichopeza americana,* on the other hand, has a green color and is irregularly marked with dark lines and blotches (Fig. 97) which serve remarkably well to break up the visual outline of the insect. And while larvae of *Oropeza* conceal themselves well down in the moss by day and feed almost wholly at night, *americana* often browses at the surface in full daylight. Larvae of *americana* may also be found more deeply in the moss by day, but it is a rare occurrence to find an *Oropeza* larva exposed to view.* Occasionally the irregularly-shaped, green and brown larvae of *Liogma nodicornis* (Tipulidae: Cylindrotiminae) are found on the same moss with *Dolichopeza americana,* and a similarly-colored and patterned moth caterpillar (Noctuidae—my identification) was three times taken together with these two species of tipulid larvae, all providing striking examples of protective resemblance of insect to environment. It seems clear to me that there is a correlation of color pattern in *Dolichopeza* larvae with the time of active feeding.

Locomotion.—In the field the collector will probably find larvae of *Dolichopeza* in an inactive state in which the anal lobes are withdrawn and the head is retracted within the second and/or third thoracic segments. This is the attitude assumed by the larva in reaction to tactile or light stimuli, as it shrinks from both. In this position, the larva may remain quite motionless for many minutes. When the irritation has eased or ceased, the larva puts out its head, protrudes the anal lobes and proceeds to a place of concealment. Lacking any sort of creeping welts such as are found on larvae of some other genera of Tipulidae, the larva of *Dolichopeza* accomplishes locomotion by three other means. It may move slowly by extension and contraction of the body, using the rough skin and large bristles as braces against the surrounding medium. More rapid locomotion is achieved by the pushing action of the anal lobes in combination with bodily undulations. Sometimes the head is extended forward and a moss stem or other support is grasped between the mandibles, so that the body may be pulled forward by contraction. This method of getting around is occasionally used alone but more often simultaneously with one or both other means described.

Preparation for pupation.—Larvae not feeding at the moss surface will ordinarily be found just beneath the surface in fairly well formed tubes. Close examination of such a tube shows that it is constructed not by the larva's having eaten or forced its way through firm material or dense moss but rather by caulking larger, pre-existing cracks with a frass of digested moss fragments and other debris. Larvae do not penetrate more than a few millimeters into wood or soil upon which their moss habitat occurs, and they have never been found in any but the most spongy, soft wood in advanced stages of decay. A tube thus formed is of course usually

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* To collect larvae from mosses brought into the laboratory, I have spread the mosses in a pan, leafy surface upward, and covered them with a few sheets of dampened newspaper. After a few hours in this artificial darkness, larvae may be found feeding at the surface of the moss.

closed behind the larva and is shifted from place to place according to available food and appropriate sites. But in the last days of its fourth stadium, the larva prepares a more compactly walled tube, oriented roughly parallel to the moss surface and with an open anterior end curving up to the surface. It is within this tube that pupation occurs and the pupal stage is spent. The pupal burrow is usually about one and a half times as long as the pupa but has been found as short as one and a quarter times the length of the pupa in *Dolichopeza subalbipes* and as long as twice the pupal length in *venosa*.

Pupation.—As the pupa takes shape within the skin of the fourth instar larva, the larval head capsule is pushed slowly forward and downward. In an individual about to undergo the transformation from larva to pupa (that is, the actual molt), the pupal structures become visible through the larval cuticle only a few hours before ecdysis. The head capsule becomes sharply deflected downward, about two hours prior to the molt, until its longitudinal axis forms an acute angle with that of the body generally (Fig. 98), stretching the skin of the prothoracic dorsum taut. The lobes surrounding the spiracular disc are drawn together in such a way as nearly to conceal the spiracles. A period of about fifteen minutes of relative inactivity was noted to precede the molt, following which occurred an abrupt resumption of movement, terminating after only a few minutes in the splitting of the old head capsule and prothoracic skin and the rapid emergence of the pupa. Worked off backwards by bodily undulations of the pupa, the old larval skin is pushed into the back of the burrow, in the form of a small, blackish, wrinkled wad, scarcely recognizable from surrounding frass and other debris, except for the head capsule. With some knowledge of the usual length of the pupal burrow, one ordinarily may recover the shed last larval skin rather easily by watching for the head capsule. If the skin is not recovered and preserved within a couple of days after pupation, however, decomposition sets in, and various organisms, chiefly mites and Collembola, begin to feed on it, destroying all but the strongly sclerotized head.

Seasonal distribution.—It has been my repeated observation that not only is the late summer generation of adults composed of individuals smaller than those of the spring generation, for reasons presented earlier, but also that there are fewer flies in the late summer generation. Several explanations for this are possible, such as the likelihood of a greater amount of parasitism or predation on larvae during the summer, or starvation or desiccation of larvae due to summer drouth conditions. It seems not improbable, however, that it may be due, at least in part, to differential rates of larval development; that is to say, some larvae in favorable habitats complete all their growth stadia, pupate and produce the fall generation adults, while others in more marginal habitats possibly attain the fourth larval instar but are prevented from growing rapidly enough to pupate in late summer and as a result overwinter as larvae. The result of this would be a spring generation of adults derived from larvae some of which are approximately nine months old and others of which are nearly a year old. Intensive field observation of larvae at a particular locality through an entire year would probably provide an answer to this problem.

The seasons for collecting larvae in various instars have been discussed under the heading of collection and preparation of material for study.

Exploration of larval habitats during the spring, summer and autumn shows that the larvae seldom penetrate more than a few millimeters, perhaps a centimeter, below the surface of their bryophyte food supplies and then only into soft substrata such as rotten wood or soil. I was curious to know where they spent the winter, whether still near the surface or deep beneath the moss, burrowing downward like the immature stages of some other kinds of insects. Plainly, those larvae that lived in the shallow growth of moss covering boulders or rock cliffs could not go very far from the surface to escape winter's cold. And there are not many places in the northern parts of the range of the genus where larvae could go below the frost line. In order to answer this question, I marked several microenvironments (that is, particular patches or hummocks of moss) found to contain numerous larvae in late summer and fall and revisited these in midwinter. While some of the larvae had gone a short distance below the surface, most were in about the same places where they had been active during warmer weather. From moss solidly frozen in a cake of ice that was chopped from the floor of a marsh in Michigan on 31 December, I succeeded in rearing *Dolichopeza sayi*. A larva thawed from the ice slowly extended its contracted body as it warmed in the laboratory, and after a few hours it was actively feeding. By 30 January, this larva had developed into an adult fly.

By remaining at or near the surface, larvae are able to take advantage of occasional warm days, in late autumn and early spring, to feed. Furthermore, drainage of the microenvironment is sufficient in most instances to protect the larvae from becoming frozen within a formation of ice; but even if so frozen, they are able, at least some of the time, to survive. Physiological adaptations, such as supercooling, reduction of body water with consequently higher salt concentration in the haemolymph, adsorption of water on protein molecules, an so on, surely enable the larvae to withstand many of the low temperatures to which they are subjected. It is not inconceivable that in their contracted state they are able to conserve at least for a while minute amounts of radiant heat received at times when there is no snow cover. In spite of all this, I believe winter weather does take an appreciable toll, for the spring populations of larvae are much reduced from those of the autumn, and there is not likely to have been extensive predation in winter.

Ecological distribution.—It is possible to describe the general habitats of the various species of *Dolichopeza* in rather broad terms, such as swamps and marshes, rocky ravines, mesic woodlands, and the like; but what is actually described in these cases is the kind of place in which adults of the species may be found. These habitats, for the various species and species groups of *Dolichopeza*, have already been discussed under the natural history of adults. Within or adjacent to these broad and not always well-defined types of habitats, the microhabitats of the larvae may be widely distributed or narrowly restricted.

Larval microhabitats have been discovered for all North American species of *Dolichopeza*, except the two new species described herein, and in all cases the food substance was a moss or liverwort, although larvae may occasionally be found in the various substrata upon which the bryophyte is growing (cf. Alexander, 1920: 981). Larvae of most species of *Dolichopeza* have been observed to feed on a variety of bryophytes, a variety that will surely be found vastly increased as observations are continued. It might therefore appear that the distribution of a particular species is controlled by the distribution of the bryophytes upon which its larvae can subsist. This, however, is only partly true. Whatever mosses or liverworts are utilized by *Dolichopeza* as larval habitats are those the microenvironmental characteristics of which are to a large measure conditioned by the general environment in which they are growing. While it is true that most bryophytes have fairly limited ranges of ecological tolerance, some grow under various conditions. Therefore, it does not follow that, if larvae of a species of *Dolichopeza* have been found feeding on a particular kind of moss, whereever that moss occurs there will be found also the fly. For example, *Leucobryum glaucum* growing loosely and luxuriantly on hummocks in a birch-maple swamp is a known, albeit uncommon, larval habitat for *Dolichopeza obscura;* but I would not expect to find *obscura* larvae in that same species of moss growing, as it does much more often, in compact, dry cushions on the floor of a hilltop oak-hickory woods. *Hedwigia albicans,* growing usually on exposed rocks, is a dry, blackish moss that seems an unlikely habitat for any crane fly larva. But if the rocks were in a wooded area, shaded by trees, the moss could retain enough moisture to support larvae of *Dolichopeza tridenticulata,* a species much more tolerant of dry conditions than any other in the genus (see Alexander, 1920: 983, under *Oropeza obscura*).

That it is the conditioning effect of the general environment on the microhabitat and not the general environment itself that governs the distribution of larvae of *Dolichopeza* is shown by the fact that where appropriate microhabitats obtain in contrasting kinds of general environments the crane flies may be found. *Dolichopeza sayi,* for example, seems to find the ecological conditions required by its immature stages rather generally available along the shaded borders of northern swamps and marshes, and its larvae are found widely scattered there in the mosses of the swamp floor and hummocks. By contrast, in an area of rocky ravines, where *sayi* is present in much smaller numbers and where adults were seen only in a limited area of vegetation in the bottom of a ravine, larvae were found only around one small patch of swampy soil, only a few square feet in extent, below a permanent seepage from the cliff. It is thus not the swamp type of general environment that limits the distribution of the species. As a further example, larvae of *Dolichopeza tridenticulata* occur in great numbers in thin growths of moss on boulders and rocky walls of gorges in southern Indiana and Ohio, but the species also finds a vastly more limited yet somehow satisfactory habitat in a sparse growth of moss in crevices of tree bark in a woodland on comparatively level ground, in southern Michigan.

Precisely what the larvae need from their surroundings has not been studied in detail. Their reactions in the laboratory to excess moisture and to desiccation have supplied some information, however, about their ecological requirements. Very young larvae are easily drowned in even a small amount of water, when they are unable to extricate themselves from it. If its moss habitat becomes flooded, a larva in an advanced stage of development first closes together the upper and lower lobes of its spiracular disc, then extends its caudal end up to the surface, exposing the spiracles to the open air. The surface of the disc is very smooth and apparently repels water, while the lobes surrounding it so effectively hold back the surface film of the water that the disc may actually be withdrawn very slightly below the surrounding water level without being wetted. A submerged larva also extends its head, making the body fully outstretched.* If the water does not soon recede, the larva begins to crawl toward a drier place, periodically pausing and putting its spiracles to the surface for air.

If a larva is removed from damp moss and placed in an empty dish or on a tabletop, it will wander about aimlessly until the cuticle dries. At this point, the larva retracts its head and anal lobes, decreases the exposure of its spiracular disc by drawing the lobes closer together, and contracts its entire body, thus reducing the evaporation surface. Movement ceases, and unless restored to a moist environment the larva will continue to lose body fluids through the skin and will shrivel and die on that spot.

In view of these reactions to drying and excessive wetting, one may make some generalizations about the bryophyte habitats of larvae of *Dolichopeza*. It seems unlikely, for example, that primarily aquatic mosses, such as *Fontinalis* or some species of *Drepanocladus* or *Hygrohypnum* would be utilized. The same could be said of mosses that ordinarily grow in dry places, such as *Grimmia*, *Ceratodon* and *Hedwigia*, although it has been shown that such mosses may, when their usual ecological situation is modified, support these larvae. It of course follows from this that whatever bryophytes are utilized must not at any time during the larval part of the crane fly life cycle become inundated or desiccated for a prolonged period, if the larvae are to survive. On the other hand, it seems not unlikely that larvae do perish as a result of oviposition in such fluctuating, marginal microhabitats that happened to have been in a favorable condition during the season for oviposition.

Larvae of *Dolichopeza* were sought in all kinds of mosses and liverworts available, as well as in soil, decayed wood, fungi and other plants, leaf litter, and the like. They were found in a wide variety of bryophytes, which demonstrates a certain latitude in their ecological tolerance, but some generalizations about their habitat preferences may be gained also, I believe, from the bryophytes in which they were not found. Aside from never having been found in aquatic or in very dry mosses, as discussed above, they were never collected either from loosely-growing, bushy mosses

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* This initial reaction to inundation is useful in obtaining over-all measurements of living larvae.

or from those that grow in tightly-arranged tufts or patches. I suspect that the very compactly-growing mosses, such as *Bryum argenteum* or *Ceratodon purpureus,* even if growing in the appropriate environment, would offer too much resistance to the tunneling larvae, while the loosely-growing mosses, such as *Climacium, Rhodobryum, Polytrichum* and most *Mnium cuspidatum,* present too diffuse a framework for the construction of burrows by the caulking method described earlier.

Not only the growth habit of the bryophyte but also its leaf texture affects the crane fly's selection of microhabitat, or at least its choice of food. Coarse-leaved mosses like *Polytrichum* were always rejected, when offered to larvae in laboratory rearing dishes, and apparently are not eaten under natural conditions. Bryophytes with thick leaves, such as the thallose liverworts, seem not to be eaten either. In a mixed growth of leafy *Mnium punctatum* moss and the thallose liverwort, *Pellia epiphylla,* larvae of *Dolichopeza americana* fed exclusively, as far as could be determined by field observation, on the *Mnium.*

It scarcely need be mentioned that mosses which do not occur anywhere about the various general environments of *Dolichopeza* are not likely larval habitats. These would include some moss species that usually grow on sand or clay in open fields, in seashore habitats, and other unforested places. Many such mosses were collected and examined, however, during the early stages of this investigation.

Where several species of *Dolichopeza* occur within one general environment, as is usually the case, each species has its characteristic larval microhabitat, although these often overlap broadly, resulting at times in the occupation of a single clump of moss by larvae of as many as three species. In a swarm of adults under a rock ledge in a wooded ravine, I may find together adults of *Dolichopeza obscura, tridenticulata, polita, walleyi* and *americana.* A search for the immature stages might show, however, that *obscura* came from *Hypnum* moss growing on a rotten log, *tridenticulata* from *Dicranella* on the rather dry upper surface of a large boulder, *polita* from mixed *Tetraphis* moss and powdery lichen on the moist undercut surface of the rock outcrop, *walleyi* from *Plagiothecium* growing as a mat on the rich soil of the floor of the ravine, and *americana* from *Mnium* growing on the damp rock at the base of the cliff.

More than fifty species of bryophytes have been found associated with larvae of *Dolichopeza,* ranging from rather dry *Dicranella* on boulders to decidedly wet *Amblystegium* of swamps, from calcareous, marl-forming *Gymnostomum* to acidic *Sphagnum,* and from fairly compact cushions of *Tetraphis* to the loose mats of certain liverworts or the low, leafy clumps of *Mnium.* In general, these microhabitat plants are those through which the larvae can move freely but which are at the same time compact enough to permit burrow formation * and which are not excluded for any of the reasons stated above.

Certain species of *Dolichopeza* have so far been found usually in mosses that were only damp, while other species have always been collected from wet mosses. A correlation between species of crane fly and the amount of moisture in its larval habitat can be indicated by a rather arbitrary arrangement set forth in Table 3. In this table, known food plants are arranged from the driest at the top to the wettest at the bottom. As many mosses will grow under diverse conditions, they are entered in the table according to their relative water content at the time of collection. The species of *Dolichopeza* are arranged from left to right across the top of the table in the order which I believe expresses their increasing affinity for moisture. Mosses in particular but liverworts as well are often found growing in close associations of two or more species. The following mosses and liverwort were collected together with food plants listed in the table and are possible or probable food sources for the larvae, although the relationship has not been established: *Anomodon attenuatus, Anomodon rostratus, Aulacomnium palustre, Brachythecium* sp., *Dicranella* sp., *Dicranum flagellare, Drepanocladus aduncus, Lophcolea heterophylla, Mnium cuspidatum, Thuidium delicatulum* and *Thuidium recognitum.*

Although several larval microhabitats have been discovered, there must be a great many more still unknown. When I compare, in the field, the number of adults on the wing with the number of pupal skins found (or the number of larvae that could have been found at an earlier date), it sometimes seems to me that I have scarcely touched upon their major moss habitats, that I might have overlooked the most important places. This of course is largely a result of the diffuse distribution of the immature stages and the concentration of adults in places not always near the larval habitats.

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* So often do the larvae follow lines of least resistance in moving through moss that a convenient way to collect them from fairly compact cushions is to bend the leafy outer surface of the moss into a convex curve until it opens along naturally formed cracks. In these cracks will be found nearly all the larvae which inhabit the particular bit of moss.

A systematic arrangement, by family, of the habitat bryophytes listed in Table 3 illustrates something of the range of plants of this phylum that are utilized by larvae of *Dolichopeza.* Eleven of the twenty-seven families of mosses known from North America are represented, and of those not appearing here many are specialized families including only a few species. The family Hypnaceae, by far the largest in this continent, is not disproportionately represented by the sixteen listed species. In contrast to the broad distribution of food plants among the mosses, all five species of liverworts fall into a single family, the Jungermanniaceae, or leafy liverworts, which are not unlike mosses in leaf texture. The other five families are so far unknown as *Dolichopeza* habitats, and it seems that most of the liverwort habitats yet to be discovered will also be species of the Jungermanniaceae.

MOSSES

Sphagnaceae: *Sphagnum palustre, Sphagnum* sp.

Georgiaceae: *Tetraphis pellucida*

Polytrichaceae: *Atrichum macmillani, Atrichum undulatum*

Fissidentaceae: *Fissidens taxifolius*

Dicranaceae: *Dicranella heteromalla, Dicranum scoparium, Leucobryum glaucum*

Grimmiaceae: *Hedwigia albicans*

Tortulaceae: *Desmatodon obtusifolius, Didymodon tophaceus, Gymnostomum calcareum*

Orthotrichaceae: *Orthotrichum sordidum*

Bryaceae: *Leptobryum pyriforme, Mnium affine, Mnium punctatum, Mnium* sp.

Leskeaceae: *Myurella careyana*

Hypnaceae: *Amblystegium riparium, Amblystegium varium, Brachythecium salebrosum, Bryhnia graminicolor, Campylium chrysophyllum, Entodon cladorrhizans, Eurhynchium pulchellum, Eurhynchium serrulatum, Heterophyllium haldanianum, Hypum curvifolium, Hypnum imponens, Hypnum lindbergii, Hypnum* sp., *Plagiothecium denticulatum, Plagiothecium deplanatum, Plagiothecium roeseanum, Platygyrium repens.*

LIVERWORTS

Jungermanniaceae: *Calypogeia trichomanis, Chiloscyphus pallescens, Geocalyx graveolens, Plagiochila asplenioides, Scapania nemorosa.*

In examining bryophytes for the larvae of *Dolichopeza,* one repeatedly comes across certain other organisms, mostly arthropods but, if the plants are from wet habitats, molluscs as well. Those most regularly found in association with *Dolichopeza* larvae are small pyralidoid caterpillars (identified by Mr. H. W. Capps), various stratiomyid larvae (unidentified, occurring in wet mosses especially), several species of Collembola (Entomobryidae, Po-

TABLE 3.—Distribution of Larvae of Species of North American *Dolichopeza* in Bryophyte Microhabitats Arranged According to Moisture Content

BRYOPHYTE HABITAT	Species of *Dolichopeza*												
	trident'ata	polita	americana	venosa	obscura	johnsonella	subvenosa	walleyi	subalbipes	carolus	similis	sayi	dorsalis
Hedwigia albicans, on rocks	×												
Dicranella heteromalla, on upper surface of boulder in woods	×												
Orthotrichum sordidum, in crevices of tree bark, in woods	×												
Tetraphis pellucida, with powdery lichen, shaded sandstone cliff	×	×	×										
Calypogeia trichomanis, on shaded sandstone cliff		×											
Atrichum macmillani, on sandstone cliff		×	×										
Leucobryum glaucum, near base of sandstone cliff in woods		×	×										
Dicranella heteromalla, near base of sandstone cliff		×	×										
Bryhnia graminicolor, on exposed clay bank			×										
Plagiothecium roeseanum, on trapped soil, sandstone cliff		×		×									
Hypnum sp., on trapped soil, sandstone cliff		×											

Platygerium repens, on bark of fallen tree, in hardwoods								×					
Myurella careyana, on sandstone cliff		×											
Plagiochila asplenioides, on sandstone cliff		×	×										
Eurhynchium serrulatum, on trapped soil, sandstone cliff		×											
Scapania nemorosa, on sandstone talus rock		×											
Mnium punctatum, at base of damp sandstone cliff		×	×										
Atrichum undulatum, on glacial till slope								×					
Chiloscyphus pallescens, on glacial till slope					×								
Leptobryum pyriforme, at base of wet sandstone cliff				×									
Mnium sp., on damp soil, bank of brook, in woods							×						
Campylium chrysophyllum, on wet sandstone cliff		×											
Desmatodon obtusifolius, on wet sandstone cliff		×											
Tetraphis pellucida, on swamp hummocks					×				×		×		
Geocalyx graveolens, on swamp hummocks									×				
Plagiothecium deplanatum, on stream bank in woods								×					
Entodon cladorrhizans, on clay soil, stream bank								×					
Leucobryum glaucum, on bank beside spring			×							×			

TABLE 3.—Distribution of Larvae of Species of North American *Dolichopeza* in Bryophyte Microhabitats Arranged According to Moisture Content—*Concluded*

BRYOPHYTE HABITAT	Species of *Dolichopeza*												
	trident'ata	polita	americana	venosa	obscura	johnsonella	subvenosa	walleyi	subalbipes	carolus	similis	sayi	dorsalis
Tetraphis pellucida, on bank beside spring			×							×			
Hypnum imponens, on soil beside stream, in woods			×					×					
Dicranum scoparium, on hummocks in swamp									×		×		
Hypnum curvifolium, on hummocks in swamp					×								
Leucobryum glaucum, on hummocks in swamp					×								
Heterophyllium haldanianum, on rotten wood, in swamp					×						×	×	
Plagiothecium denticulatum, on tree bases, in swamp											×		
Fissidens taxifolius, on boggy, shaded soil					×								
Gymnostomum calcareum, in seepage over sandstone		×				×							
Amblystegium riparium, at margin of woods pool								×					

Mnium affine, at margin of woods pool								×					
Didymodon tophaceus, on sandstone, at waterline												×	
Eurhynchium pulchellum, at margin of swamp, on soil												×	
Brachythecium salebrosum, swamp margin, on soil												×	
Hypnum lindbergii, on wet soil at edge of swamp												×	
Sphagnum palustre, wooded zone of bog													×
Sphagnum sp., bog, at edge of tree zone													×
Amblystegium varium, on floor of marsh												×	×

duridae and Sminthuridae), and numerous species of Acarina, notably the "beetle mites" (Oribatoidea) and parasitoid mites. Of these, the lepidopterous larvae are worthy of further comment, here, for their trails through the mosses may often be mistaken for those of *Dolichopeza.* These caterpillars usually had reached a length of about 5 to 8 mm. by the time I first noticed them, and I saw some over a centimeter long, which I took to be later instars. The caterpillars are of a reddish brown color, sparsely haired, with large, glossy brown heads. They are extremely active creatures and ravenous eaters of moss. Their tunnels in the moss are frequently lined with webby silk fibers and are always littered with fecal pellets, which is what makes them resemble the trails of *Dolichopeza.* I feel fairly certain that these common pyralidoid caterpillars are the immatures of small, light brown or light grayish moths that are often taken in the rearing dishes. Mr. Sherman Moore, of Detroit, has identified several of the moths as *Crambus alboclevellus* Zell. (from *Mnium cuspidatum*), *C. elegans* Clem. (from *Aulacomnium palustre*), *C. albellus* Clem. (from *Amblystegium varium*), and *Crambus* sp. (from *Dicranum scoparium*).

Mosses and liverworts while harboring many kinds of organisms appear to furnish food directly to only a few, such as the moth larvae just mentioned and certain kinds of Tipulidae. From the rock gorge habitats, I have reared *Tipula* (*Oreomyza*) *ignobilis, Tipula* (*O.*) *fragilis, Liogma nodicornis, Limonia* (*Dicranomyia*) sp., *Erioptera* (*Symplecta*) *cana* and *Gonomyia* sp. From mosses of northern marsh borders, *Tipula* (*Yamatotipula*) *sulphurea, Tipula* (*Trichotipula*) *oropezoides* and *Limonia* (*Dicranomyia*) *immodesta* were reared, together with *Dolichopeza sayi.*

In a discussion of the ecological relationships of the larvae of *Dolichopeza,* it seems appropriate to mention associations of larvae of various species within the genus, for it often happens that the larvae, like the adults, keep close company. Within an area of *Tetraphis* moss no more than three inches in diameter, for example, may be found larvae of *americana, polita* and *tridenticulata.* Larvae of *obscura* and *subalbipes* often occur together in the mosses of swamp hummocks. Other such associations are suggested in Table 3. The important thing about these close interspecies associations is that there appears to be no competition whatsoever. There seems to be always enough moss to feed all the larvae and to keep them comfortably apart from one another. Rarely does a natural growth of moss contain so many larvae that noticeable defoliation results; in fact, I have observed only one such occurrence, in which several larvae of *Dolichopeza americana* and *Liogma nodicornis* feeding on a thin growth of *Mnium punctatum* on a sandstone cliff had conspicuously damaged an area perhaps four inches in diameter. If larvae do encounter each other occasionally during their tunneling, it seems unlikely that competition in the form of fighting would result. Even when several larvae are confined in a dish without moss, they do not show any aggressive behavior (such as is known among some other tipuline larvae) and could be described in general as lethargic. In view of these facts, it is difficult to imagine what form interspecies competition among larvae might take.

Parasites and predators.—Probably the most important difficulties with which the life of the larva is beset, except for the rigors of weather already mentioned, are predation and disease (including parasitism). There would be no point to enumerating those organisms that might prey on *Dolichopeza* larvae. The survey of predators on the Tipulidae in general given by Alexander (1920:721 ff.) will suggest several possible ones. The only time I have actually witnessed predation on a *Dolichopeza* larva was an instance of *D. walleyi* attacked by a larva of a small species of *Tabanus* * in the moss *Hypnum imponens* growing at the edge of a woodland pool in southern Michigan.

Evidence of parasitism is as rare as that of predation, and there are no established records of parasites in or on the larvae of *Dolichopeza*. Certain hymenopterous parasites that become evident only during the pupal stage of the crane fly host (see section on pupal life history) must occur within the larva throughout its life but do not hinder its activities and allow it to grow and metamorphose. In rearing dishes I have found the braconid wasp, *Macrocentrus reticulatus Muesebeck,* and an ichneumonid, *Mesoleptus* sp. † Concerning these, Dr. Muesebeck wrote: "The *Macrocentrus* must be a parasite of some lepidopterous larvae although no host seems yet to have been recorded for *M. reticulatus*. For species of *Mesoleptus* we have little host information. There are some records of the rearing of specimens of this genus from Diptera but I do not know how authentic these are."

Parasitism in certain crane flies other than *Dolichopeza,* which were observed, may be relevant here, inasmuch as the larvae involved were taken in microhabitats of *Dolichopeza*. Perhaps the

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* Identified by Dr. W. W. Wirth, U. S. National Museum.

† Dr. Muesebeck identified the braconid, which was the first male of the species to come to his attention. Miss L. M. Walkley determined the ichneumonid.

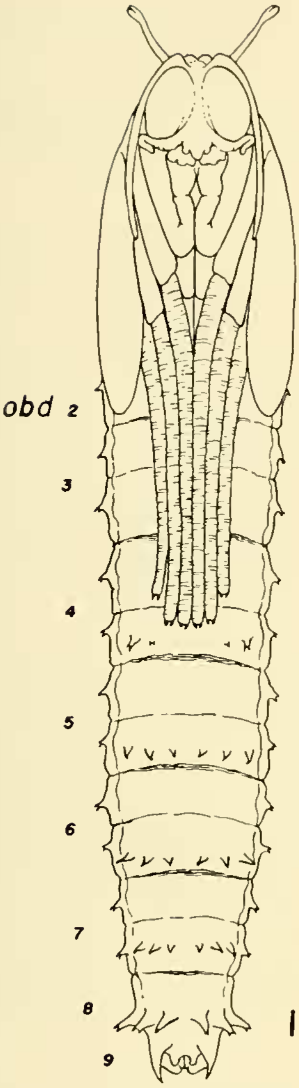
most spectacular case was that of a nematode infestation of a larva of *Tipula,* found in a moribund condition. Two large, whitish nematodes, one nearly 20 mm. long and the other over 30 mm. in length, were subsequently found to have pierced the body wall of their 16 mm. host and just completed their escape. Postmortem examination of the larva showed the internal organs to be intact but the usual sheet of fat absent. The skin around the two exit holes was thickened and blackish, and the larva was left quite limp and somewhat flattened. This is the first instance of nematode infestation of a crane fly larva to come to my attention, although it must be a common occurrence in nature.

A bacterial infection causing eversion of a portion of the caudal end of the digestive tube has been observed in three species of tipuline larvae. Internal symptoms include nodular growths on all major portions of the alimentary canal. From these whitish cysts, smears were prepared. The contents were found to consist of many small, fat-like globules and highly motile, short rod bacilli, which proved to be gram negative. Colonies of the bacilli on blood agar were gray-buff in color, with a definitely cleared zone eight millimeters in width surrounding them. While this disease kills larvae within two days of appearance of first symptoms, I was not successful in inoculating larvae of *Dolichopeza* with the bacilli.

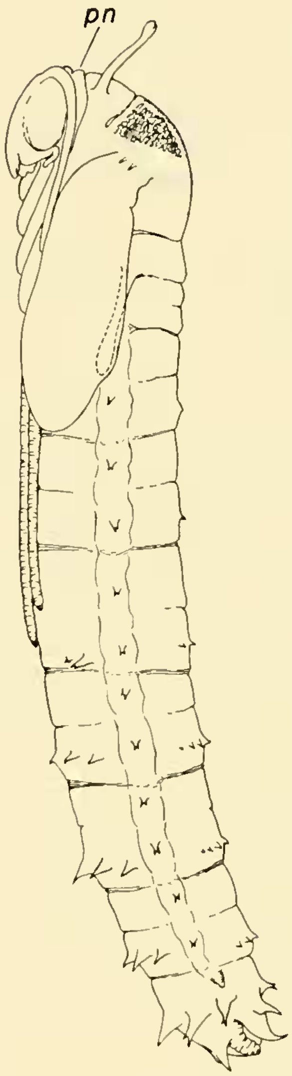
PUPAE—MORPHOLOGY

Size of the pupa depends upon both species and environment and is directly proportional to and smaller than the size of the fourth instar larva, just before pupation (Fig. 99). Pupae of the smaller species (*americana, dorsalis* and *tridenticulata*) are commonly only 10 or 11 mm. long, while those of larger species (such as *similis*) reach lengths of 16 mm. or more. Measurement of both whole pupae and cast pupal skins is subject to the same sort of error as occurs in measurement of the other life history stages, due to the position of the insect—whether outstretched, contracted, how curved, and so on. There is always a certain amount of guesswork involved, to which experience may lend some reliability. The accompanying illustrations of the pupa (Figs. 100, 101) were prepared from a specimen killed in hot water and thus slightly more than normally extended.

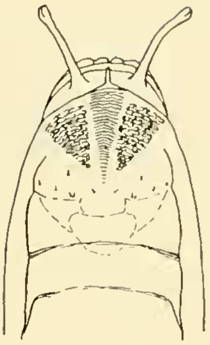
No structures on the pupal head appear to be characteristic of *Dolichopeza* alone. The shape and position of the eyes and antennal sheaths, the rather triangular labrum, and the generally-flattened aspect of the entire head are typical of pupae of the sub-



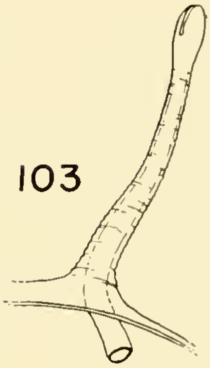
100



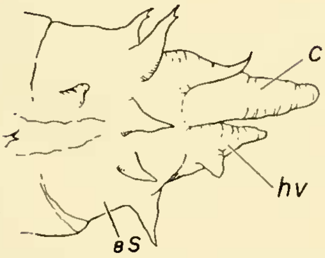
101



102



103



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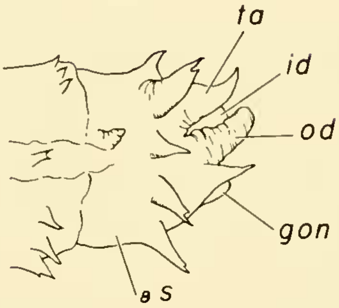

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FIG. 100. Pupa of *Dolichopeza (Oropeza) walleyi*, ventral aspect, indicating abdominal segmentation; abd—abdominal segment. FIG. 101. Same as 100, left lateral aspect; pn—pronotum. FIG. 102. Same as 100, dorsal aspect of thorax. FIG. 103. Mesothoracic respiratory horn of *Dolichopeza (Oropeza)* sp. FIG. 104. Cauda of pupa of *Dolichopeza (Oropeza)* sp., female, left lateral aspect; cr—cercus, hv—hypovalve, 8s—eighth sternum. FIG. 105. Same as 104, male; gon—gonapophysis, id—inner dististyle, od—outer dististyle, ta—tergal arm, 8s—eighth sternum.

family Tipulinae. The cephalic crests are small, as in most species of *Tipula*. In having the tips of the sheaths of the maxillary palpi recurved, *Dolichopeza* differs from its nearest North American relatives, *Brachypremna* and *Megistocera*, and from more distantly related *Tanyptera* and *Longurio*, but resembles *Nephrotoma* and most forms of *Tipula*.

Aside from the respiratory horns, the most conspicuous features of the thoracic dorsum of the pupa are two rough-surfaced, reticulated areas (Fig. 102) which are useful in recognition of the genus. However, it should be pointed out that certain species of *Tipula* possess similar reticulated areas on the pupal mesonotum (cf. Alexander, 1920: 977). *Tipula ignobilis*, for example, a species that often occurs in mosses containing pupae of some kinds of *Dolichopeza*, is so marked; but in this species, as well as in the other species of *Tipula* pupae I have seen having such a reticulation on the thoracic dorsum, the pattern of wrinkles extends anteriorly around the bases of the respiratory horns and onto the pronotum. In *Dolichopeza*, on the other hand, the reticulation is confined to the mesonotal cuticle posterior to the pseudosuture, where it occurs as roughly triangular areas in the subgenus *Oropeza* (but weakly developed in *subvenosa*) or more oblong patches in *Dolichopeza americana*. The dorsal mid-line of the mesonotum is characterized by a low, anterior carina, behind which are a series of transverse ridges or folds crossing the mid-line in the region between the reticulated areas.

There are half a dozen pairs of exteremly small spines on the mesonotum, disposed approximately as shown in Figure 102. Takahashi (1958: 121) has found the number of pairs of these spinules useful in distinguishing pupae of certain Japanese species of *Oropeza*, but in the North American species their taxonomic use is impracticable. While at the outermost position, in *Dolichopeza subalbipes*, there are ordinarily two spines together, the pattern for the other species closely resembles that figured. Occasionally a spine may be broken off or missing altogther, or there may be only one where in the corresponding position on the other side two occur together.

The metathorax is narrow and, where exposed dorsally, rather closely resembles the first abdominal segment. Only the proximal ends of the sheaths of the halteres are exposed, in the subgenus *Oropeza*, the remainders being normally concealed beneath the wing sheaths. In *americana*, however, the sheaths of the halteres are fully exposed but closely applied to the posterior edges of the wing sheaths.

Close behind the head is the very narrow prothorax, which in this genus is distinctly separated from the mesothorax. The respiratory horns, which are of rather uniform shape throughout all the species and which are ordinarily referred to in literature on the Tipulidae as "pronotal breathing horns," are not situated upon this prothoracic segment. Alexander (1920: 752), describing the tipulid pupa in general, said: "Immediately behind the head on the pronotum are the two breathing horns. . . ." In the taxonomy of pupae of Tipulidae, the term "pronotal breathing horns" persists even to the present time (see, for example, Wood, 1952: 81, etc.). The respiratory horns, however, are situated on the pupal mesonotum, between its anterior margin and the pseudosutures (which in the adult are indicated by the pseudosutural foveae, or humeral pits). Dissection of the pupa when the developing adult within is fairly well formed clearly shows the relationship of parts of the imaginal thorax to the areas of the pupal thorax as here identified. Furthermore, the tracheal tube leading from the respiratory horn connects to the mesothoracic spiracle of the developing adult.

A most peculiar difference exists between pupae of *Dolichopeza polita* and all the other North American species of the genus in the appearance of the tracheal connection between the respiratory horn and the spiracle. In most species, this tube is rather straight, making a direct connection, while in *polita* it is greatly convoluted and folded back upon itself, its length easily twice the distance from the base of the breathing horn and the spiracle (Fig. 107). This condition is found in all three races of *polita*. The only other occurrence known to me is in the pupa of *Dolichopeza* (*Nesopeza*) *geniculata* Alexander, which I found projecting from a growth of liverwort on the slope of the volcanic peak, Halla San, on Cheju Island, Korea, in the fall of 1954. I know of few other characteristics in any stage of *Dolichopeza* that so completely set apart one species from all others in a continental fauna.

The first abdominal segment of the pupa is short and indistinctly divided, while the next six segments are formed of broader, well-marked basal and caudal, or anterior and posterior portions. The basal rings lack spinous processes on the dorsal and ventral surfaces but have these present on the pleural folds. The posterior rings bear, in addition to the pleural spinous processes, transverse rows of more or less conical projections, in varying numbers, on the dorsal surfaces of all segments and the ventral surfaces after the third or fourth segment. The eighth abdominal segment is not differentiated into rings. It bears four * large, subconical, spine-tipped projections on its sternal surface and four slightly smaller ones dorsally, and it has the pleural spinous process present only in the "posterior ring" position. On the dorsolateral surfaces of the eighth abdominal segment, near its anterior edge, there are two low, blunt lobes, one at each side. Unlike the other projections of the pupal abdomen, these lack spinous tips and apparently are homologous with the fleshy lobes occurring in a similar position in the larva. This supposed homology seems correct, inasmuch as the lobes described are characteristic of pupae of species of *Oropeza* but do not occur in *Dolichopeza americana.* These lobes are lacking also in other genera of the Tipulinae, so that the same feature, in a sense, can be used to separate both larvae and pupae of *Oropeza* spp. from those of *Tipula, Nephrotoma* and allied genera.

Sheaths of the various hypopygial elements of the adult comprise the greater part of the caudal segment of the pupa. In the female these (sometimes termed the acidotheca) rather closely resemble the terminal abdominal structures of the adult (Fig. 104). In the male pupa (Fig. 105) the sheaths bear less resemblance to imaginal structures, although the relationship of corresponding parts is clear. Comparison of Figures 111 and 112 shows a conspicuous difference between male pupal terminal structures of *Dolichopeza americana* and species of *Oropeza.* The base of the sheath of the outer dististyle is adjacent to that of the tergal arm in *Oropeza* spp. (Fig. 111), but these two structures are distinctly separated basally in *americana* (Fig. 112). The differences in spinous tips of the caudal sheaths and projections of the eighth segment apparent in these two figures are not reliable for subgeneric recognition, as there is too great an amount of variation in these parts.

Recognition of species in the pupal stage of *Dolichopeza* would seem, from a cursory survey of structures, to be a fairly easy undertaking. The unfortunate truth is, however, that very little can be salvaged for taxonomic use at the species level from the described array of bristles, spinous projections and other apparently taxonomically useful features. With only a scattering of species or a small number of specimens at hand, one might soon find some character in which the available pupae differ. Complications ordinarily arise, however, when larger numbers of specimens are examined,

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* Rarely will this number vary, but see Figure 38.

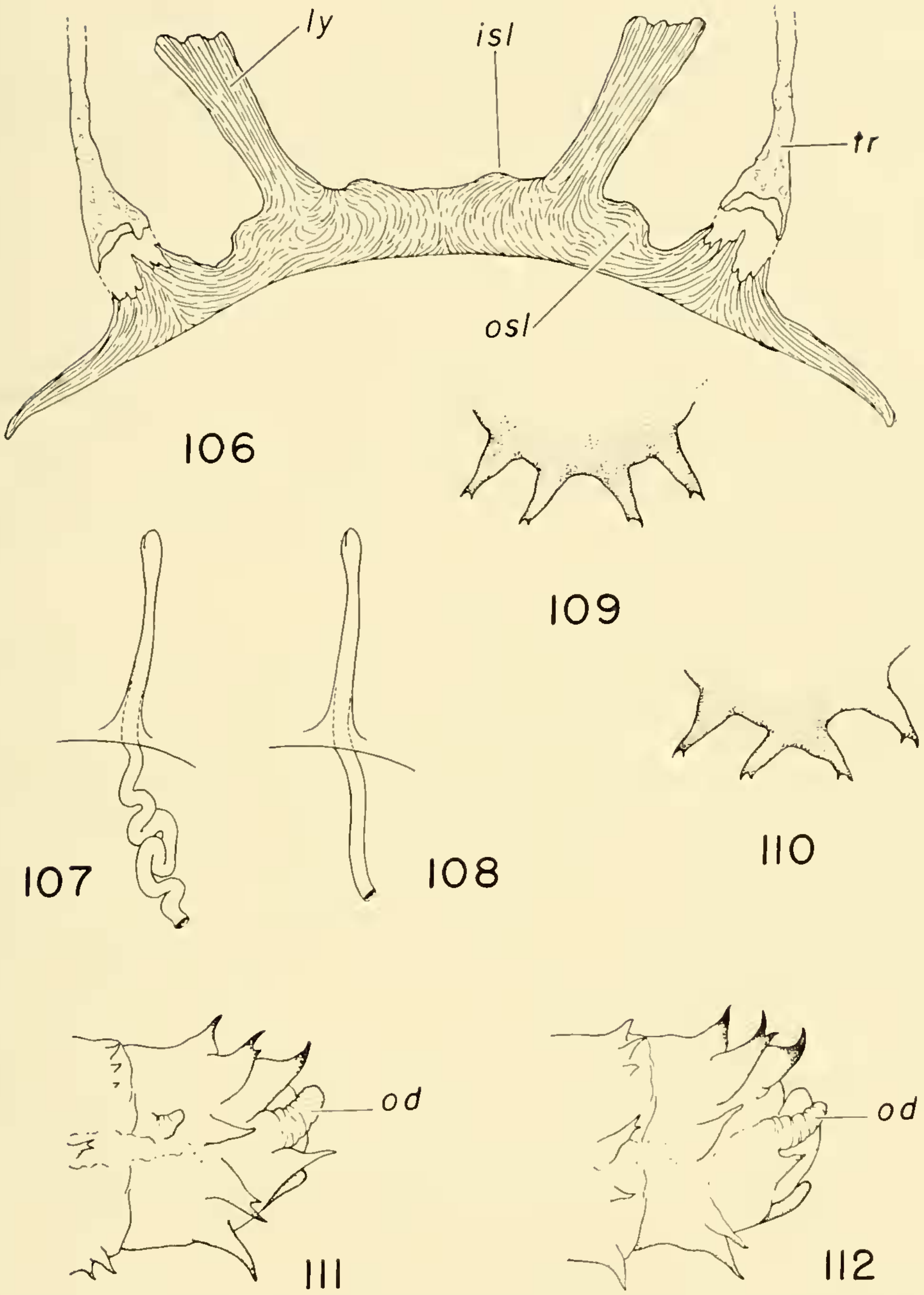


FIG. 106. Spiracular yoke of pupa of *Dolichopeza (Oropeza) similis;* isl—inner secondary lobe, ly—lobe of yoke, osl—outer secondary lobe, tr—larval tracheal trunk. FIG. 107. Mesothoracic respiratory horn and tracheal connection to spiracle in *Dolichopeza (Oropeza) polita* sspp. FIG. 108. Same as 107, *Dolichopeza (Oropeza) tridenticulata.* FIG. 109. Arrangement of spinous processes of eighth abdominal sternum of pupa of *Dolichopeza (Oropeza) sayi* group. FIG. 110. Same as 109, *Dolichopeza (Oropeza) obscura* group. FIG. 111. Cauda of male pupa of *Dolichopeza (Oropeza)* sp., left lateral aspect. FIG. 112. Same as 111, *Dolichopeza (Dolichopeza) americana.*

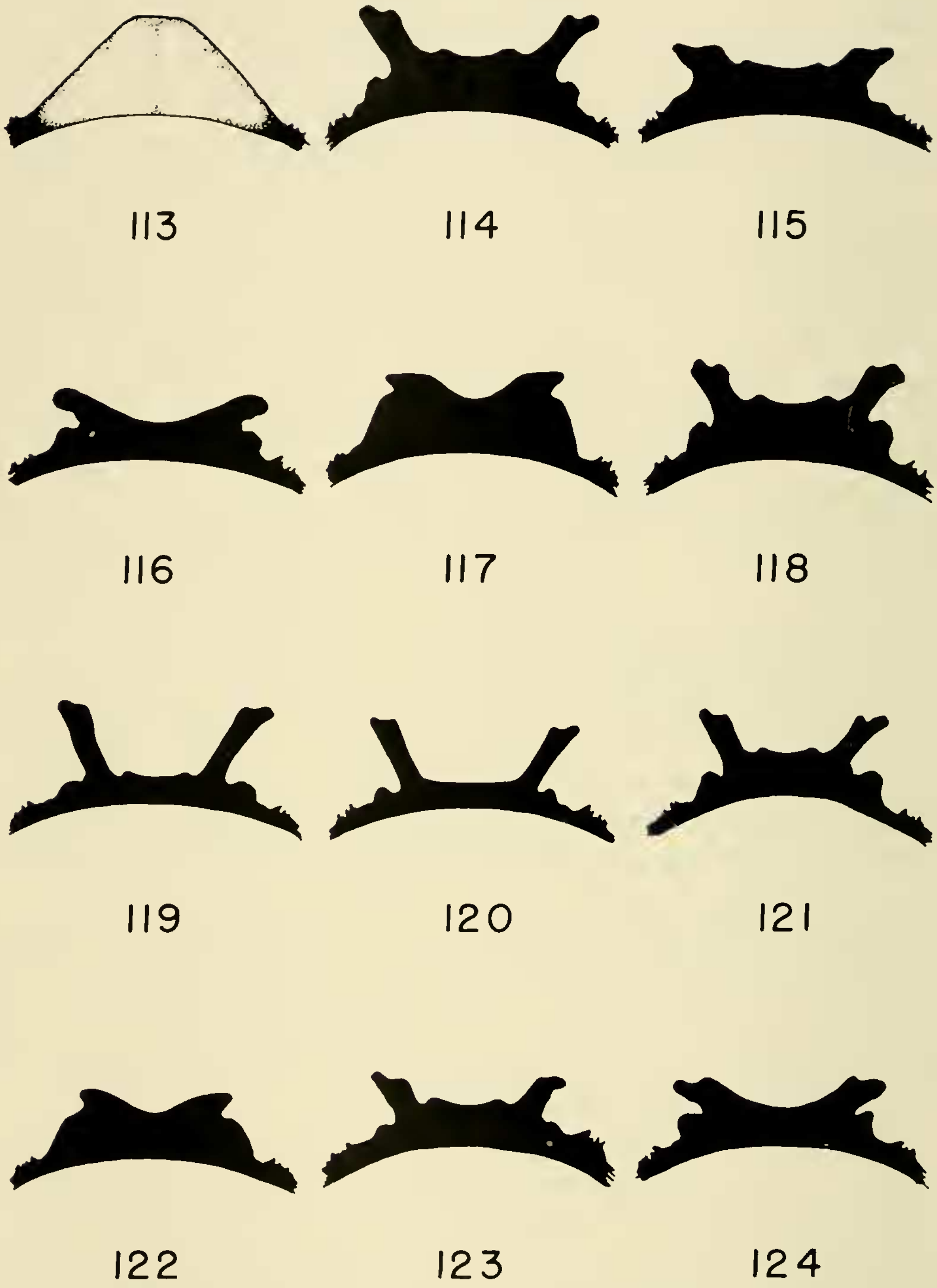
especially when these represent species of a very uniform group. In some characters, like the bristles of the mesonotum already mentioned, there is too much uniformity throughout the genus, while in others there is as much variation within one species as there is among species. An example of the latter is the number of spine tipped projections on the fifth, sixth and seventh abdominal sterna. The count of these conical points may vary from species to species and from row to row; but on one species, the count of projections in a certain row was found to vary from 8 to 13, complicated by partial fusions, branching, irregular spacing and unusual sizes of projections. As a further example, the spinous projections of the eighth abdominal segment may be single or multiple tipped and may be hooked and variously provided with bristles; but an examination of variation in the tip of a particular projection in a single species showed that the tip varied from two to four branched and that bristles were either present or absent.

One species group within the genus can, however, be separated on the basis of characteristics of the pleural spinous processes. In *Dolichopeza carolus, dorsalis, obscura* and *subalbipes,* these processes are rather blunt-tipped, with an apical bristle that nearly equals the length of the subconical, basal part of the process. In the remaining species, these processes have bifid tips, one of the branches usually short, the other longer and very sharp, with the apical bristle arising in the notch between the two points. Species in the *obscura* group usually have the two medial projections of the eighth sternum originating from a common base or with their bases contiguous (Fig. 110), while in the *sayi* group these projections are ordinarily spaced apart, their bases not touching (Fig. 109). This character is not wholly reliable, exceptions having been seen, but it applies in general. Another character that is nearly always reliable is the presence or absence of spinous projections on the posterior ring of the fourth abdominal sternum. In certain species, these are present and from half to nearly equal the size of those on the fifth segment, whereas in the other species they are absent altogether or represented only by bristles.

One additional character, of a completely different sort, permits separation of species when used in conjunction with the group characters just noted. To my knowledge, this character has never been observed prior to this study and consequently is new to the classification of crane fly pupae. Just posterior to the median projections of the eighth abdominal tergum, there is an infolding of the pupal skin, a sort of pouch or pocket, flattened dorsoventrally, situated with its closed end directed cephalad in such a way as to be rather readily visible through the eighth tergum, especially in cast pupal skins immersed in alcohol. Microscopic examination of this structure reveals that tiny "stress lines" in the surrounding pupal cuticle converge into the pocket and that the remains of the larval spiracles are attached to the strongly sclerotized arch formed by the converging folds of cuticle (Fig. 106). Although I have not studied the development of this pouch, it seems to be intimately associated with, perhaps a result of, the withdrawal of the larval spiracles at the time of pupation, when the tracheal outlet shifts from a caudal to thoracic position. Since the entire structure seems to me to act as a rigid bar connecting the two spiracles and bringing about their coincident displacement, I have suggested the name "spiracular yoke" for the pouch and related cuticular thickenings at its sides (Byers, 1958: 136). The spiracular yoke in both males and females has a characteristic shape, within limits, for each species, and a study of many specimens indicates that certain features of the yoke are reliably constant. Figures 113 through 124 show something of the variation of the spiracular yoke from species to species. It is not practicable to attempt to describe the variation within each species, but it should be pointed out that the illustrations provided are composites, each based upon several pupae. In the key, reference is made only to the general form of the yoke, such as whether its lobes are elongated or short and whether there are inner, secondary lobes (Fig. 106, isl). I have observed the spiracular yoke also in other genera (*Brachypremna, Megistocera* and several species of *Tipula*), where it is again distinct for the species examined. Perhaps it will prove to be a character of general application in the classification of the pupae of Tipulidae.

TENTATIVE KEY TO PUPAE OF NORTH AMERICAN *DOLICHOPEZA*

Pupae are most easily studied in alcohol. Pupal skins preserved dry should be soaked a few minutes in alcohol, then cleaned of adhering moss particles, soil and other debris before being studied. Skins thus prepared may be flattened with a blunt needle so that the spiracular yoke is seen in the proper profile. Whole pupae may require removal of the eighth and ninth abdominal segments, which separate easily from the imaginal tissue after the fourth day of the pupal stage. Adult genitalia thus exposed may identify the species; the spiracular yoke, at any rate, is made more readily visible. Live pupae, given a few days, will provide their own identification.



FIGS. 113-124. Spiracular yokes of pupae; 113—*Dolichopeza (Dolichopeza) americana*, 114—*Dolichopeza (Oropeza) carolus*, 115—*Dolichopeza (Oropeza) dorsalis*, 116—*Dolichopeza (Oropeza) obscura*, 117—*Dolichopeza (Oropeza) polita*, 118—*Dolichopeza (Oropeza) sayi*, 119—*Dolichopeza (Oropeza) similis*, 120—*Dolichopeza (Oropeza) subalbipes*, 121—*Dolichopeza (Oropeza) subvenosa*, 122—*Dolichopeza (Oropeza) tridenticulata*, 123—*Dolichopeza (Oropeza) venosa*, 124—*Dolichopeza (Oropeza) walleyi*.

The following key is limited in several respects. The pupal instar of *Dolichopeza johnsonella,* as well as that of the two new species described herein, is unknown. Probably *johnsonella* will "key out" near *subalbipes.* Pupal skins identified as those of *carolus* and *subvenosa* were not obtained from reared specimens but were identified on the basis of circumstantial evidence, as explained later under the respective species headings. Only four female pupal skins thought to be of *subvenosa* and three male and three female skins regarded as of *carolus* were found. The pupae of *dorsalis* and *similis* are known from only about half a dozen specimens each, but of the remaining species several to many pupae have been found and studied.

1. Reticulated areas of mesonotum oblong in shape; no blunt lateral lobes on anterior portion of eighth abdominal tergum; spiracular yoke roughly triangular in shape and weakly sclerotized except at edges (Fig. 113) . . . . *americana*
   Reticulated areas of mesonotum triangular in shape; a blunt lateral lobe anteriorly on each side of eighth abdominal tergum; spiracular yoke variously shaped, usually with two conspicuous lobes, strongly sclerotized throughout 2
2. Tracheal tube connecting respiratory horn with adult spiracle strongly convoluted . . . . *polita* sspp.
   Tracheal tube straight 3
3. Pleural spinous processes of second through seventh abdominal segments blunt-tipped, bearing a single apical bristle about as long as basal portion of process 4
   Pleural spinous processes of second through seventh abdominal segments mostly bifid at tip, with at least one sharply-pointed branch and with apical bristle arising from notch between branches 7
4. Middle projections of eighth abdominal sternum set apart so that the four are about evenly spaced (Fig. 109); spiracular yoke shallowly and irregularly emarginate, the lateral lobes shorter than their width at base (Fig. 115) . . . . *dorsalis*
   Middle projections of eighth abdominal sternum set closer together than distance from either to outer projections, or divergent from a low base common to both (Fig. 110); spiracular yoke relatively deeply emarginate, the lateral lobes longer than their width at base, 5
5. Lobes of spiracular yoke only about one and a quarter to one and a half times as long as their width at base, their tips variously rounded; emargination between lobes usually smoothly curved (Fig. 116) . . . . *obscura*
   Lobes of spiracular yoke from one and a half to three times as long as their width at base, their tips irregularly truncated, often expanded and notched; emargination between lobes more angular or irregular 6
6. Basal part of spiracular yoke deep, or thick, the emargination between lobes irregular by reason of inner secondary lobes (Fig. 114); middle projections of eighth abdominal sternum clearly separated

at base; spinous projections on fourth abdominal sternum present, about one-third to one-half as long as those on fifth sternum; projections on fifth through eighth sterna very darkly tipped . . . *carolus*

Basal part of spiracular yoke usually shallow, or slender, the emargination between lobes not interrupted by secondary lobes (Fig. 120); middle projections of eighth abdominal sternum set very close together or arising from low base common to both (Fig. 110); usually no spinous projections on fourth abdominal sternum, those of fifth through eighth sterna not all darkly tipped . . . . *subalbipes*

7\. Middle projections of eighth abdominal sternum set close together or divergent from a low base common to both (Fig. 110); spiracular yoke broadly and shallowly emarginate, the lobes shorter than their width at base, sometimes with an apical papilla (Fig. 122), *tridenticulata*

Middle projections of eighth abdominal sternum set apart so that the four are about evenly spaced; lobes of spiracular yoke slightly to much longer than their width at base 8

8\. Spinous projections on fourth abdominal sternum usually conspicuous, about one-half as long as those on fifth sternum, or longer 9

Spinous projections on fourth abdominal sternum usually inconspicuous or absent, sometimes represented by bristles 11

9\. Lobes of spiracular yoke only about one and a half times as long as their width at base, often bluntly rounded at tips; emargination between lobes rather smoothly curved (Fig. 124) . . . . *walleyi*

Lobes of spiracular yoke about twice as long as their width at base, their tips usually slightly expanded and notched; emargination between lobes more angular, often irregular due to presence of inner secondary lobes 10

10\. Reticulation on mesonotum distinct, occurring in roughly triangular areas; spiracular yoke as in Figure 123 . . . . *venosa*

Reticulation on mesonotum obscure, mostly in form of low, transverse wrinkles or folds similar to those along mesonotal mid-line; spiracular yoke as in Figure 121 . . . . *subvenosa*

11\. Lobes of spiracular yoke about three times as long as their width at base; emargination between lobes deep and angular, with small inner secondary lobes; basal portion of yoke slender, not thick (Fig. 119) . . . . *similis*

Lobes of spiracular yoke one and a half to two times as long as their width at base; emargination between lobes angular, sometimes irregular due to inner secondary lobes, but not deep; basal portion of yoke thick (Fig. 118) . . . . *sayi*

PUPAE—NATURAL HISTORY

In nearly all rearing experiments, the length of the pupal stadium in *Dolichopeza* was six days, which is about average for the Tipulidae generally. Occasionally the period was found to be seven days, and one female of *Dolichopeza venosa* spent eight days in the pupal condition, indoors, but did not emerge normally and died in the process. In the laboratory, the time of emergence was artificially altered, that is to say postponed, by exposure of pupae to bright light or to chilling. It therefore seems reasonable to believe that naturally occurring fluctuations in environment could effect changes in the length of time that the fully formed adult insect within the pupal skin would remain there. It would be interesting to know, for example, whether *Dolichopeza* adults emerge at the end of a six-day pupal stadium, if that time happens to coincide with an all-night rainstorm.

Although it is essentially in a resting state, in which many larval structures disintegrate and the adult anatomy takes shape, the pupa is capable of considerable activity at nearly any time during its existence. Vital physiological activities of the insect must, of course, proceed without interruption; and even as it frees itself of the last larval skin the pupa may be seen to have already a fully-formed and functioning tracheal system and a regularly-pulsating dorsal vessel, both visible through the smooth, pale integument. Pupal activities in ecdysis show that at least a part of the muscular system also is already in operation. In the absence of artificial stimulation, however, the pupa usually remains quiescent, only occasionally wriggling to the opening of its tube and perhaps projecting slightly from it. This movement is accomplished by dorso-ventral undulations of the abdominal segments behind the tips of the wing sheaths, which by their stout spinous projections gain a firm hold in the moss.

Since the pupa lives in the same microhabitat as the larva, little comment needs to be added concerning its general ecology. Each pupa lives in isolation within a burrow often scarcely more than half again as long as the pupa itself. Where moss habitats have been favorable for the development of several larvae, the pupal burrows may be numerous and often crowded, as for example at one place where I found three pupal skins of *Dolichopeza polita* ssp. projecting from one square centimeter of moss surface.

Predation and parasitism.—The relatively defenseless pupae would seem to fall easy prey to several kinds of predators that live in mosses or feed rather generally over the surface of the ground. Only once, however, did I actually find evidence of predation on a *Dolichopeza pupa.* As I was examining a rearing dish, I saw a pupa of *Dolichopeza similis* come wriggling up out of the moss in a most hurried manner. When I saw that its two posterior segments had been nearly torn away, I probed its tube in the moss and discovered a twenty millimeter larva of some species of Elateridae.*

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* Alexander (1920:729) reports elaterid larvae feeding on a dead larva of *Tipula trivittata.*

Larvae of *Bittacus apicalis* (Mecoptera) found foraging in moss containing pupae of *Dolichopeza americana* and *polita* were probably seeking only dead pupae or other such decomposing material, as they fed readily on dead pupae and refused living ones when both were offered as food.

Several instances of parasitism of pupae by chalcidoid wasps were noted in the course of rearing experiments. At first, the infested pupae were found dead, broken open at one or more places, with half a dozen or more tiny, spindle shaped larvae busily consuming both the pupal contents and the necrotic edges of the openings in the skin. These larvae were about two millimeters in length, pale at the ends, with a broad, pale spotted band of tan showing through the smooth, transparent skin of the middle region. It appeared that these larvae were only scavengers, there being no direct evidence of parasitism. Yet I wondered why the number of them feeding on any one pupa was always about the same and why they were never found feeding on dead larvae in the same rearing dish.

Attempts to rear these supposed parasites invariably failed, until on 11 June 1952 I found in one of my dishes a newly-formed pupa of *Dolichopeza walleyi*, through the pale integument of which I could see the familiar larvae at work. Inspection showed that the pupal skin was intact, making it clear that the larvae were indeed parasitic. It seems that the parasites must remain very small throughout the larval life of their host and then develop rapidly as soon as the pupa is formed, for, although there is no interference with the process of pupation, by the time the pupa is only a day old it is largely hollowed out by the parasites. By 14 June, activity within the pupal skin had ceased, and two days later the whitish pupae of the wasps could be seen. On 17 June, the reddish eye pigment of the parasites became visible, and between evening of 19 June and morning of the next day there occurred an abrupt change in color of the parasites, the eyes turning deep red and the bodies nearly black. Between 10:00 a. m. and 3:30 p. m. on 23 June, about a dozen tiny wasps emerged through a small hole in the side of the fly pupa. These were identified by Dr. B. D. Burks of the U. S. National Museum as belonging to an undescribed species of *Tetrastichus* (Hymenoptera: Eulophidae).

Similar wasps were subsequently reared from a pupa of *Dolichopeza americana*, in which instance, however, there were only seven parasites. Other species of *Dolichopeza* parasitized by *Tetrastichus* sp. include *obscura* and *subalbipes*. All cases of infestation by this parasite were observed in May and June, but there is as yet no reason to suspect that pupae of the fall generation are not also parasitized. Rogers (1933: 35) reports braconid parasites in the pupa of *Dolichopeza walleyi* (as *Oropeza sayi*); however, as none of these wasps was preserved, there is no way to be sure whether what he actually observed were also *Tetrastichus*.

It seems probable that the mites often found on adults of *Dolichopeza* congregate on the pupa and attach themselves to the body of the imago as it emerges from the pupal skin.

Pupal development.—The newly-formed pupa is pale tan in color, often with a greenish tinge showing through, especially from the abdominal contents. The dorsum of the thorax is usually a slightly darker tan or brown than is the rest of the pupa, and the thoracic respiratory horns are quite dark brown from the outset of pupal life. During the first few hours of the pupal stadium, the eyes are pale, but the violet-purple pigment of the developing ommatidia within slowly diffuses across, beneath the pupal eye covering, so that at the end of the first day the pupal "eyes" are fully colored and have a brick red appearance. As the individual lenses of the developing adult eye are clearly visible through the pupal skin, it may be seen that the compound eye does not initially form directly beneath the pupal eye cover but is displaced slightly anterolaterally. Within the wing sheaths, the veins sometimes glisten as if filled with air, and the membrane appears as a dark, strongly-convoluted, compactly-folded mass.

As the pupa grows older, its colors become darker, the greenish hue of the abdomen being replaced by brown in most species of *Oropeza* but remaining in *americana* and to a lesser extent in *dorsalis* and *subalbipes*. The thoracic breathing horns become very dark brown with black tips, and the low median carina of the mesonotum takes on a black color in many species. As the adult body takes shape, some parts of the pupal skin are left apparently empty, or nearly so, by the contraction of the initially rather amorphous tissue of the young pupa into the smaller and more compact adult structures. The hypopygial elements largely pull out of their formative sheaths, and the rostrum, maxillary palpi, antennae and other parts loosen from their sheaths, so that by the end of about four days of the pupal stadium the developing adult is separated almost completely from its pupal covering.

Very marked changes in over-all appearance are undergone by the pupa shortly before the adult is to emerge. When the pupal skin grows rapidly darker brown in color and becomes dry and shiny, emergence of the adult may be expected within the following eight to twelve hours. At this time, the coloration especially of the head, thorax and wing and leg sheaths becomes noticeably darker, somewhat resembling dark amber-brown glass. Eye color changes from brick red to almost black in only a few hours. On the surface of the wing sheaths, the characteristic pattern of venation of the adult wing, in miniature, can easily be made out in reflected light. In the laboratory, pupae often moved one-third to half out of their tubes at the onset of this drying and darkening period, but I have not been able to verify that they do so under natural conditions.

Emergence of adult.—Emergence of the adult is a rapid process, requiring only a few minutes. I have twice had the good fortune to observe emergence from its earliest moments, when the pupal skin first began to split, and have witnessed by far the greater part of the process on several other occasions. In preparation for emergence, the pupa moves out of its burrow far enough to expose the anterior one-third to one-half its length. After a time, the pupal skin parts in two places: a transverse split between the antennal sheaths and the pronotum, from the mid-line behind the head down to the sheaths of the front legs, and a longitudinal split along the dorsal mid-line, across the occipital portion of the head, the prothorax and the mesothorax almost to the metathorax.* Then, for a few seconds, the adult insect, still fully encased, swallows air in order to expand and lengthen its body. Air is taken into the abdominal part of the ventriculus but much more extensively into the membranous crop, which in one fly killed a few seconds after emergence was found distended so as to fill the abdomen back to the anterior edge of the fifth segment. As a consequence of this inflation, the adult body rises from the pupal skin rapidly and without apparent exertion, until the wings are drawn free of their sheaths, the femora are fully exposed, and approximately the anterior half of the abdomen has emerged (Figs. 125, 126). Although the compressed neck quickly extends, the head remains bowed, with the antennae and maxillary palps directed downward. The wings are not withdrawn as crumpled structures but, somewhat in the manner of an opening parachute, spread to their full expanse as fold after fold of the membrane is drawn taut by the pull from outside. During the minute or less that is required for emergence to the point of freeing the wings, almost the only motion noticeable is the slight tugging action of the coxae.

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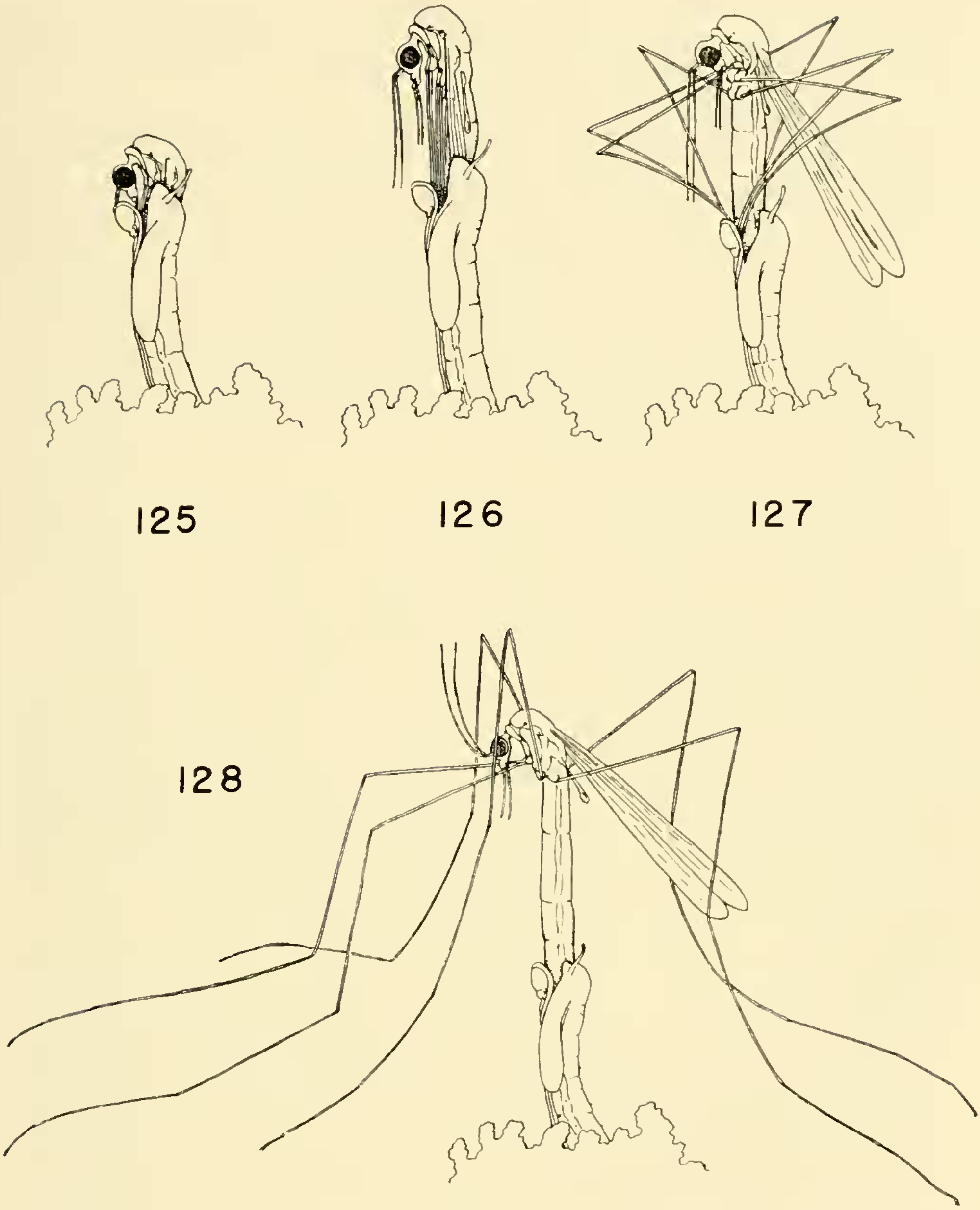
* The coverings of head and antennae are left attached to the rest of the pupal hull by only a thin, membranous skin and sometimes break off as a unit, a sort of mask.



FIGS. 125-128. Successive stages in the emergence of the adult of *Dolichopeza (Oropeza) polita* ssp. from the pupal skin.

With the greater part of its body free of the pupal skin, the fly begins a rocking motion, combining dorso-ventral movements and extensions and contractions of the abdomen. The legs are withdrawn with somewhat less exertion, the joints between femora and tibiae flexed first out to the sides (Fig. 127), then high overhead, as the long tarsi are pulled free. As the legs are freed, the tip of the abdomen remains fast in the pupal skin, the wings are kept folded over the back, and the antennae are directed upward (Fig. 128). Then, with its feet braced against the moss and its wings fluttering weakly, the fly suddenly breaks completely away from its pupal hull, moves a short distance over the moss surface, and pauses to rest, with legs outspread and the weight of the thorax and abdomen directly on the moss.*

The soft and almost colorless sclerites begin to harden and take on slight color in a matter of minutes, while the body size reduces by discharge of swallowed air and of the last of the copious greenish meconium, the fluid wastes resulting from pupal metabolism. Most of the meconium is expelled during emergence, leaving the pupal skin almost a quarter full of the greenish fluid, unlike the condition found in most Tipulinae, which leave their pupal skins empty. It may be a quarter of an hour before the fly attempts to take to the wing, and it seems that in its natural surroundings the newly-emerged fly must be easy prey for all manner of predators that are active at night.† Within two or three hours, the fly is well colored and hardened and is capable of sustained flight. Its full coloration develops in about six to eight hours following emergence, although because of callowness of body the fly may be considered teneral for a longer period of time. With emergence, the life cycle begins anew. Figure 99 summarizes the stages of development, indicates the approximate rate of growth, and illustrates the changes in body size as the insect passes from egg through the larval instars, pupation and emergence as an adult fly.

KEY TO ADULT MALES OF NORTH AMERICAN *DOLICHOPEZA*

1. Wings without discal cell (cell 1st M_2); cross-vein m-cu joining media before its first branching (Fig. 2); ninth tergum without lateral arms (Fig. 129) .... subgenus *Dolichopeza;* note that the male of *D.* (*D.*) *borealis* new species is so far unknown; see discussion of that species .... *americana*

Wings with discal cell normally present; cross-vein m-cu joining the media beyond its first branching (Fig. 1); ninth tergum with lateral arms .... subgenus *Oropeza* 2

2. Gonapophyses shaped like small knobs, bearing decurved, stout black spines and bristles (Fig. 6) .... *obscura* group 3

Gonapophyses with tips flattened and blade-like or slender and pointed, sometimes with hairs but never with stout black spines, *sayi* group 10

3. Tarsi white and femora and tibiae pale with narrowly darkened tips; body coloration yellowish marked with dark brown or black; wings with intense brown stigmal spot; ninth tergum as Figure 208 or 209 .... *subalbipes*

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* In instances of emergence from pupae in mosses on the undersides of rock ledges or on vertical surfaces, some variation of the described procedure is of course necessary. Such conditions, however, were not duplicated in the laboratory.

† Emergence in the laboratory usually occurred in the early hours of darkness, between 9:00 p. m. and midnight.

Tarsi dusky, brown, yellowish brown or yellowish white, but tips of femora and tibiae not contrastingly darkened; body coloration brownish with dark brown markings 4

4. Apical two-thirds of tarsi yellowish white, grading into light brown on basal third; medio-posterior margin of ninth tergum with two broad, rounded lobes and a slightly longer central tooth (Fig. 137) *australis*

Tarsi uniformly colored throughout, dusky, brown or yellowish brown and not conspicuously paler than legs 5

5. Medio-posterior margin of ninth tergum undulating, with two broad, rounded lobes; tergal arms slender and not much expanded at tips (Fig. 157); a median brush of black hairs on eighth sternum (Fig 162) . . . . *johnsonella*

Medio-posterior margin of ninth tergum with projecting teeth; tergal arms various; no brush of hairs on eighth sternum 6

6. Tergal arms widely flared and emarginate at tips; teeth of ninth tergum not set close together (Fig. 164) . . . . *obscura*

Tergal arms not flared or emarginate at tips; teeth of ninth tergum set close together, usually on a common basal projection 7

7. Outer dististyles blunt-tipped and not expanded at bases; median lobe of tergal margin subrectangular in shape, bearing three teeth of nearly equal length (Fig. 221) . . . . *tridenticulata*

Outer dististyles with pointed tips and with basal portion usually enlarged; median lobe of tergal margin various but usually with three teeth, the central one the longest . . . . *polita* subspecies 8

8. Thoracic dorsum shiny or "polished"; basal enlargement of outer dististyle darkened around the edge; median lobe of tergal margin usually slender but may vary (Fig. 171) . . . . *polita polita*

Thoracic dorsum dull and opaque, rarely slightly shiny in certain lights; basal enlargement of outer dististyle pale; median lobe of tergal margin usually distinctly three-toothed 9

9. Three teeth of median lobe of nearly equal length, the middle one slightly the longest, and all set close together; tergal arms flared about mid-length and tapering to slender tips (Fig. 188), *polita cornuta*

Three teeth of median lobe variable in length, middle tooth the longest, but teeth not always set close together; tergal arms only slightly expanded at tips but widest there (Fig. 180) . . . . *polita pratti*

10. Outer dististyles pale, shorter than inner dististyles, not conspicuously projecting (Fig. 145); tarsi white and femora and tibiae pale with narrowly darkened tips . . . . *carolus*

Outer dististyles dark or yellowish, longer than inner dististyles and conspicuously projecting; tarsi yellowish white, tan, gray or brown 11

11. Gonapophyses narrow, tapering to blackened, heavily sclerotized points; tergal arms broadly expanded and spatulate at tips; medio-posterior margin of ninth tergum with a broad, irregular projection 12

Gonapophyses not narrow and tapering to points; tergal arms and margins various but not as above 13

12. Adminiculum with a prominent, subapical, posterior (or ventral) spine (Fig. 219) .... *subvenosa*
    Adminiculum without a subapical spine (Fig. 234) .... *venosa*
13. Ninth tergum very shallowly emarginate, with undulating margin; tergal arms not expanded at tips (Fig. 149); gonapophyses short, terminating in an abrupt, spinous tip (Fig. 152) .... *dorsalis*
    Ninth tergum slightly to moderately emarginate and toothed; tergal arms slightly to markedly expanded at tips; gonapophyses longer than broad, variously expanded at tips 14
14. Gonapophyses slightly widened toward the tips, the margins entire; tergal arms only slightly expanded at tips (Fig. 195) .... *sayi*
    Gonapophyses expanded at tips, the margins irregularly toothed; tergal arms markedly expanded at tips 15
15. No prominent projections from inner faces of gonapophyses; adminiculum without spines at tip (Fig. 241) .... *walleyi*
    A long, spinous projection directed dorso-cephalad from the inner (anterior or dorsal) face of each gonapophysis; adminiculum with two small apical spines (Fig. 204) .... *similis*

KEY TO ADULT FEMALES OF NORTH AMERICAN *DOLICHOPEZA*

1. Wings without discal cell (cell 1st M_2); cross-vein m-cu joining media before its first branching (Fig. 2) ... subgenus *Dolichopeza* 2
   Wings with discal cell normally present; cross-vein m-cu joining the media beyond its first branching (Fig. 1) .. subgenus *Oropeza* 3
2. Hypovalves of ovipositor each with a heavily sclerotized apical tooth (Fig. 135); tarsi white from mid-length of first segment to apex of fourth .... *americana*
   Hypovalves of ovipositor tapering evenly to tip (Fig. 136); only about apical one-sixth of first segment and all of second segment of tarsi pale (white in hind tarsi only), third segment dusky, fourth and fifth dark .... *borealis*
3. Tarsi white; tibiae and femora pale in color, their tips conspicuously darker and sharply contrasting 4
   Tarsi dusky, yellowish brown, or brown; or, if whitish, without darkened, contrasting tips on tibiae and femora 5
4. A heavily sclerotized spot, conspicuously darker than the tip or any other part of the hypovalve, present on each side of eighth sternum (Fig. 148), approximately below the ninth or base of the tenth tergum .... *carolus*
   No such spot present, although entire eighth sternum and hypovalves may be uniformly strongly sclerotized; or spot may show weakly, in rare instances, never as strongly sclerotized as tip of hypovalve .... *subalbipes*
5. Dorsum of thorax contrastingly colored or striped, the darker portions much darker than the pleura; if striped, the stripes distinct; body coloration generally yellowish brown, the abdomen annulated with darker brown or black; legs yellowish, yellow-brown, yellowish white, or brown 6

Dorsum of thorax not contrastingly colored or striped and not conspicuously different in color from pleura; if striped, the stripes indistinct and not much darker than the ground color; general body coloration dusky brown, dark yellowish brown, or light brown, annulated with darker brown in each case; legs dusky, gray-black, dark brown, brown, or brown with pale, yellowish brown tarsi . . . 12

6. Thoracic pleura pale and unmarked (except for slight darkening of the pre-episternum in occasional specimens 7

Thoracic pleura distinctly marked, especially on the anepisternum, ventral part of pre-episternum and mesothoracic meron (see Fig. 14) 8

7. Dorsum of thorax reddish brown in color, sometimes indistinctly striped, with a narrow, cocoa-brown median stripe usually present but not clearly differentiated; flies of bogs, marsh borders and swamplands especially . . . . *dorsalis*

Dorsum of thorax marked by three distinct, reddish brown stripes on a yellowish brown ground color; principally flies of mesic woodlands, in northern and eastern North America . . . . *walleyi* (part)

8. Cubital vein scarcely, if at all, more conspicuous than other wing veins (use no magnification); stigmal spot usually not very sharply defined and not intensely colored; flies of mesic woodlands generally south of Virginia, Kentucky and southern Indiana, and west of Illinois, Wisconsin, etc. (cf. 7, above) . . . . *walleyi* (part)

Cubital vein clearly more conspicuous than any other (use no magnification) by reason of a dark seam of color along the vein; stigmal spot intense, well defined and much darker than the ground color of the wing 9

9. Tenth tergum more strongly sclerotized than cerci or hypovalves, although dark spots may be present on hypovalves and eighth sternum (Fig. 207); stripes of thoracic dorsum brown to dark brown, tending to merge behind middle of prescutum; large flies of yellowish coloration, the wings with a gold-amber tinge . . . . . *similis*

Strongest sclerotization of ovipositor is on hypovalves; stripes on thoracic dorsum dark brown, distinctly separated; wings tinged with light grayish brown 10

10. Legs dark grayish brown, the tarsi light brown; body coloration yellowish with narrow annulations at incisures of abdomen; dark coloration on hypovalves neither very intense nor widespread (Fig. 200); flies of marsh borders and swamps, especially . . . . *sayi*

Legs pale, the tarsi whitish, yellowish white, or very pale tan; body coloration tan with broad, dark brown annulations at incisures of abdomen; dark coloration of hypovalves intense and generally distributed behind eighth sternum, the posterior margin abruptly paler (Figs. 220, 237); flies of rocky areas and stream borders . . . 11

11. Flies of the Appalachian Mountain region, from northern West Virginia southward through Virginia and North Carolina to northern Georgia . . . . *subvenosa*

Flies of northeastern United States and Canada, from northern West Virginia northeastward to Nova Scotia and northwestward to Minnesota, Alberta and Yukon . . . . *venosa*

12. Legs light brown, tarsi fading to pale yellowish brown or yellowish white . . . . *australis*
    Legs and tarsi of about the same color, brown, dark brown, dusky or blackish 13
13. Pronotum, prescutum and pleura of thorax markedly lighter in color than occiput of head; antennae with the two basal segments abruptly paler than flagellum 14
    Pronotum, prescutum and pleura of thorax not much, if at all, lighter in color than occiput of head; antennae more unicolorous, or, if basal segments are pale, the flagellar segments gradually becoming darker toward the tip of the antenna 17
14. Wing tinged with golden brown, the stigmal spot darker brown, with lighter areas both before and beyond it; the larger veins also dark brown, with a seam of brown color along veins Cu and m-cu; prescutal stripes usually evident, although poorly defined; abdominal annulations distinct; an intensely sclerotized spot medially on eighth sternum at base of hypovalves (Fig. 163) . . . . . *johnsonella*
    Wing faintly tinged with light gray or grayish brown, the stigmal spot only slightly darker than the ground color; veins gray to brown, lacking seam of color along Cu or m-cu; prescutum unicolorous or nearly so; abdominal annulations indistinct; no intensely sclerotized spot near base of hypovalves, although hypovalves may be in part strongly sclerotized . . . . (*polita* subspecies) 15
15. Thoracic dorsum shiny or "polished" . . . . *polita polita*
    Thoracic dorsum usually dull and opaque, light brown or light reddish brown in color 16
16. Flies of Minnesota, western Wisconsin, Iowa, western Illinois, Missouri, Kansas, Arkansas, etc. . . . . *polita pratti*
    Flies of Indiana, eastern Illinois, Ohio, Kentucky, southern Michigan, western New York, etc. . . . . *polita cornuta*
17. Tenth tergum more densely sclerotized than any other part of ovipositor (Fig. 170); thoracic coloration usually as dark as occiput of head; stigmal spot grayish brown to brown . . . . *obscura*
    Subterminal area of hypovalves more densely sclerotized than any other part of ovipositor (Fig. 229); thoracic coloration usually slightly paler than that of occiput; stigmal spot grayish brown . . . . *tridenticulata*

Subgenus *Dolichopeza*

Dolichopeza (*Dolichopeza*) *americana* Needham

Literature references.—Dolichopeza americana Needham. Needham, 1908: 210-211, pl. 16 (wing); Johnson, 1909: 117, pl. 15 (wing); Alexander, 1919: 929, pl. 43 (wing); Alexander, 1920: 981-982; Dietz, 1921: 259; Alexander, 1922b: 61; Alexander, 1924: 59; Alexander, 1925: 172; Johnson, 1925: 32; Alexander, 1926: 239; Pierre, 1926: 9; Leonard, 1928: 698; Alexander, 1929a: 236; Alexander, 1929b: 25; Johnson, 1929: 130; Alexander, 1930a: 272; Rogers, 1930: 22; Alexander, 1931a: 138.

Dolichopeza (*Dolichopeza*) *americana* Needham. Alexander, 1936: 279; Alexander, 1940: 618; Alexander, 1941a: 295; Alexander, 1942: 210, fig. 24A (wing); Rogers, 1942: 118; Foote, 1956: 221.

Original description.—"Its expanse of wing is 21 mm. Its color is brownish, paler ventrally. Its antennae are of moderate length, with the brown flagellum consisting of ten segments, slowly diminishing in length toward the tip and beset with a few stout, black hairs. The wings are of pale brown, with venation as shown in the figure just cited (fig. 5 of pl. 16), the halteres are infuscated at tips. The legs are of the usual excessive length; femora and tibiae are brown, with white bases, and all the tarsus is white except the basal half of the first segment and the apical half of the fifth segment."

Types.—No holotype or syntypical series was specifically designated by Dr. Needham, who wrote to me, in August 1951: "The specimens of *Dolichopeza americana* went to the New York State Museum at the conclusion of my third report. Whether they have been preserved or not I do not know; some other material has been lost." No specimens of this species are now in the collection at Albany, so I must assume that the type series is lost or destroyed. However, because *americana* is readily recognized, it seems unnecessary at this time to designate a neotype.

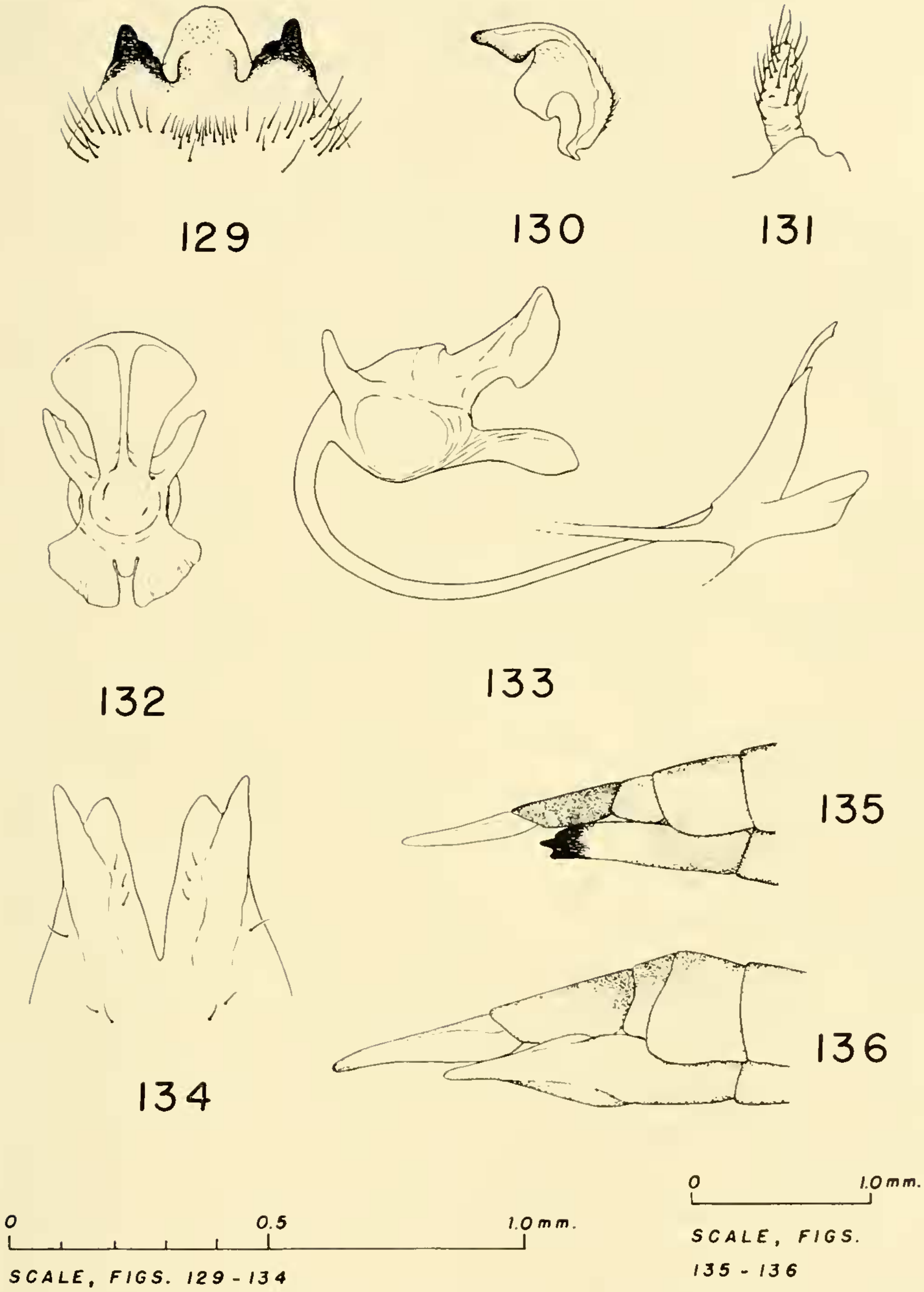
Diagnostic characteristics.—This is the most easily recognized species of *Dolichopeza*, for because of its dusky coloration, long, slender legs and white feet it is not likely to be confused with any other North American crane fly. Although it somewhat resembles *Hexatoma albitarsis* (O. S.), a species that sometimes occurs in the same general habitats, *americana* may be readily recognized in the field by its much longer and more slender legs. Its usual resting posture—hanging from overhead support by the prothoracic legs only, with the wings outspread—is also an aid in field recognition. From the only other known American species of the subgenus *Dolichopeza* (that is, *borealis*), *americana* may be distinguished by its almost completely white tarsi, as well as by certain other color and structural differences discussed under that species.

Descriptive comments.—At a distance, *americana* appears to be colored black with white feet, but at close range it is seen to be of a dark brown color dorsally, paler beneath, at the tip of the abdomen, and on the thoracic pleura, which are marked by dark spots on the mesothoracic meron, pre-episternum and anepisternum. The prescutum is indistinctly marked by three longitudinal stripes of a rich, dark brown color, while the scutellum and postscutellum are abruptly paler than all other dorsal surfaces, being a glossy grayish tan. These and other color markings of the species are frequently obscure on pinned specimens of much age. Membranous areas of the abdomens of newly-emerged females often have a greenish color, which carries over from the larval stage; this is only transitory, however, and gives way in a few days to the characteristic brown.

Venation in *americana* is extremely constant throughout the species' range, only a few abnormalities having been found among more than a thousand specimens examined. Presence of the vein Sc_1 has been noted two times, absence of a section of M_2 has been found twice, and an indication of a vein, in the form of a row of macrotrichia, projecting into cell M_3 has been seen in one specimen. I collected a specimen in North Carolina that had a spurious cross-vein in cell R_3 and in West Virginia one that had a distally directed spur vein from the m-cu cross-vein. One instance of a forked M_3 vein has been seen.

Males vary in over-all length of body from slighty over 7 mm. to about 10 mm., their wings from about 8 mm. to approximately 11 mm., nearly always just a bit longer than the body. Females average somewhat larger, the body 8.5 mm. to 12 mm., wing 8.5 mm. to 12.5 mm. All the smaller specimens were collected in August, while the larger ones were taken in June, mostly from the northern states or high in the Appalachians.

In its hypopygial structure, the male *americana* is markedly different from the species of *Oropeza*, although except for the tergal arms each part in the one finds its counterpart in the other. The ninth tergum is intensely sclerotized, emarginate medially but with a narrow, divided backward projection along the dorsum of the tenth segment (Fig. 129). Into the two deep concavities of the ninth tergum fit the strongly recurved tips of the inner dististyles. There is no *Oropeza* in which the apical portion of the inner dististyles is so reflexed or fits into the sculptured margin of the ninth tergum. The outer dististyles are shorter than the broad, basal portion of the inner dististyles, are pale straw yellow in color, and are covered with fine hairs. Viewed from above, they are slender, but they are somewhat flattened, so as to appear broader when seen from the side (Fig. 131). The gonapophyses are yellowish and are partially fused to form a trough-like backward extension of the ninth sternum (Fig. 133). Adminiculum and penis are pale yellow, less strongly sclerotized than these same struc-



Figs. 129-135. *Dolichopeza (Dolichopeza) americana;* 129—ninth tergum of male, with tenth tergum projecting from beneath, 130—left inner dististyle of male, dorsal aspect, 131—left outer dististyle, lateral aspect, 132—vesica and its apodemes, dorsal aspect, 133—vesica, penis, adminiculum and gonapophyses, left lateral aspect, 134—hypovalves of female, ventral aspect, 135—terminal abdominal segments of female, right lateral aspect. Fig. 136. Terminal abdominal segments of female *Dolichopeza (Dolichopeza) borealis* new species, holotype, right lateral aspect.

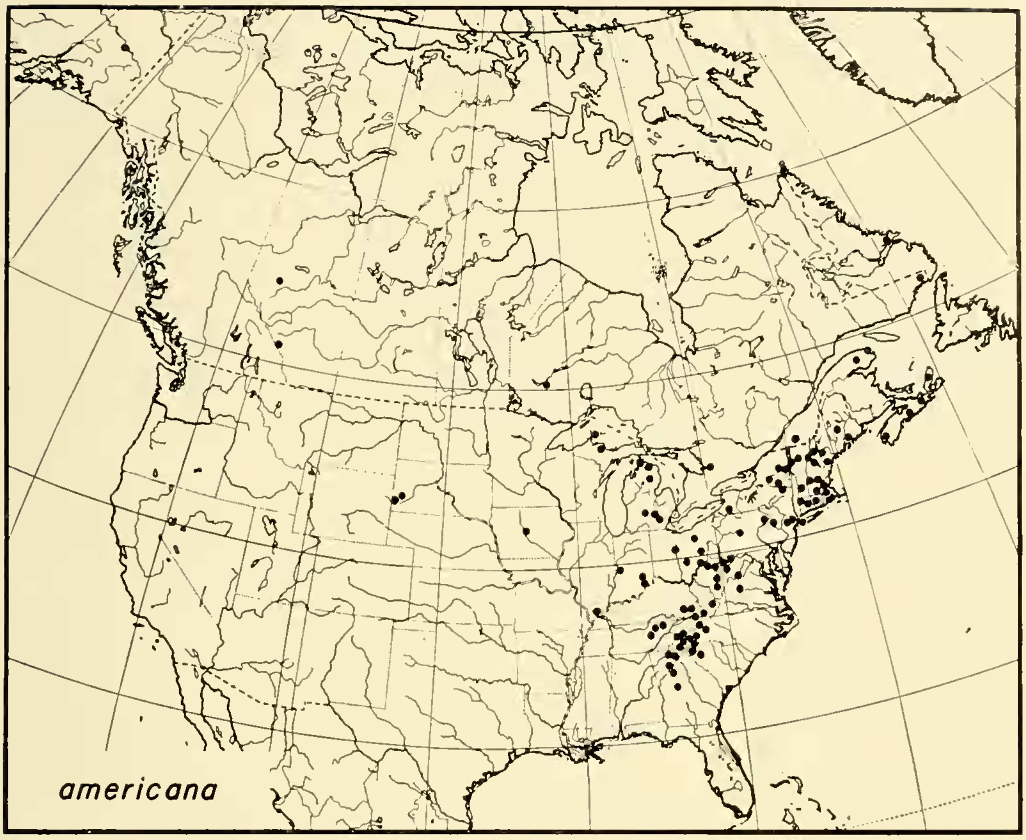
tures in any of the species of *Oropeza.* In comparison with the eighth sternum, the ninth in *americana* is much smaller than it is in any *Oropeza,* suggesting a closer relationship with certain species of subgenus *Nesopeza* in which the ninth sternum is nearly concealed by the eighth.

The ovipositor of the female *americana* is unlike that of any other species of the genus in North America, in that the hypovalves each terminate in a blackened tooth that projects beyond the otherwise truncate end (Fig. 135). Also, the ninth tergum is somewhat longer in this species than in species of *Oropeza* of comparable size.

As described by Needham, the number of antennal segments is twelve. I cannot find any evidence of fusion of the last two segments, in microscope slide preparations of the antennae, but one slide (Haywood County, North Carolina, 30 June 1924, J. S. Rogers) clearly shows thirteen segments, a small apical segment present on each antenna, as is the case in species of *Oropeza.* Alongside the lower edge of each eye, there is a conspicuous black spot. Such a spot occurs also in *Dolichopeza* (*D.*) *albipes* of Europe but is lacking in the only other American species of this subgenus, as well as in *Oropeza.* The significance of these spots is not known to me.

Geographical distribution.—At the outset of this study, the known range of this species included only eastern Labrador and the Appalachian Mountain region southward to northern Georgia, with a westward extension from New York to Michigan. However, *americana* proved to have been well named. It has the most extensive geographic range of any species of *Dolichopeza* in the world, covering over two and a half million square miles of North America, from the range described above westward into the Black Hills of South Dakota and northwestward to Alberta and the central valley of Alaska. There are, however, some wide gaps in this pattern of distribution, due at least in part to insufficient exploration. Just how the Black Hills habitat connects with the rest, if indeed it does, is not clear; this problem is discussed in the conclusions. In the Ozark-Ouachita Mountain region, there are what I regard as favorable habitats for this species, here and there, and perhaps in time the species will be recorded from that area.

Habitats.—Adults of *americana* are most often associated with rocky habitats, such as the limestone or sandstone gorges of Indiana and Ohio, the "rock houses" of the Appalachians and their foothills (Rogers, 1930: 5), and undercut or broken rock along streams in most elevated parts of eastern North America. In the



MAP 1. Range of *Dolichopeza (Dolichopeza) americana* Needham. Each spot represents one or more collections within a county (United States) or at a locality.

northern part of its range, *americana* seems to find the temperature, dampness and deep shade of its southern haunts matched in the cool forests and wet woodlands, although I have never found it to be so numerous in such habitats. Perhaps the reverse is true: that the rocky Appalachian ravines provide the "northern" microclimate in which *americana* can prosper. Individual flies are often found concentrated in small niches where suitable resting conditions prevail. For example, all individuals of *americana* taken on Harney Peak in the Black Hills were found beneath one outcropping rock, and an all-day search of the nearby forest revealed no additional flies. Again, in a southern Illinois locality, a few flies of this species were discovered in a darkened cranny, while a careful inspection of a wide surrounding area proved fruitless.

Seasonal distribution.—In those regions where I have watched and collected *americana,* I have found it the first species of the genus on the wing, both in the spring and late summer generations. In most of Ohio, Indiana and southern Michigan, it may be expected about two or three weeks after the average date of last killing frost, in the spring. This would place the peak of spring emergence in the areas mentioned at about the first to third weeks of May, depending upon local average climate, and, of course, depending upon the weather of the year. In Washtenaw County, Michigan, a pupa was collected on 13 May. Prolonged observations in a limited area in Turkey Run State Park, Parke County, Indiana, in 1953, showed *americana* present about a week before the first appearance of any species of *Oropeza.* On 18 May, ten single males and two mating pairs were observed; and on succeeding days the numbers of mating pairs increased steadily, reaching a peak of twenty-one pairs on 24 May and thereafter declining steadily. Between 18 and 29 May, only one unmated female was seen, but after 29 May, as the numbers of males diminished, the numbers of single females increased. By 9 June, *americana* had all but disappeared from the particular cranny where these observations were made and from the nearby woods. The spring population generally begins to wane, in this region, in late May to mid-June, or about ten days to two weeks after strong emergence begins, although stragglers may be netted almost any time throughout the summer, and mating pairs may be encountered, now and then, late into June. From the first generation to the second is a matter of only about ten weeks, and a second peak of emergence occurs in the early days of August, continuing for one to two weeks. For data on other parts of the species' range, see the notes on distribution, below.

Immature stages.—Eggs of *Dolichopeza* (*D.*) *americana* measure about .60 mm. x .25 mm., and a single female lays about 110 eggs. The duration of the egg stage is seven days, after which the larvae may reach the fourth instar within twenty-three days.

The larva of *americana* is the most colorful of all North American species of the genus. Its green ground color, brownish black markings and bright green spiracular disc are distinctive characteristics (Fig. 97). Lacking the dorsolateral lobes of the eighth abdominal segment, the larva of *americana* more closely resembles certain species of *Tipula* than it does its nearer relatives in *Oropeza.* It is very similar to the larva of *Dolichopeza* (*D.*) *albipes* of Europe, the only other described larva in this subgenus (see Beling, 1886: 189-191); and it may be that the closely appressed median lobes of the spiracular disc and the peculiar markings of the dorsum are characteristic of the subgenus.

Numerous larval habitats of this species have been discovered.

These vary from rather dry *Tetraphis pellucida* growing together with a powdery lichen on the undercut surface of a sandstone cliff to decidedly damp *Hypnum imponens* growing on rich forest soil beside a small stream. The ability of *americana* to survive in this broad range of habitats probably accounts for its wide distribution and leads me to expect it in many areas where it has so far not been found, such as in the Ozark Mountains. Known larval habitats of this species include, in addition to those mentioned above, *Atrichum macmillani, Leucobryum glaucum, Dicranella heteromalla, Bryhnia graminicolor, Mnium punctatum,* and the liverwort *Plagiochila asplenioides.* All these bryophytes were growing as thin coverings over sandstone cliffs, except the *Bryhnia,* which was collected from a deeply shaded clay-till bank. Feeding habits of the larva of *americana* as compared with those of *Oropeza* larvae are discussed under larval natural history.

In the pupal stage, the color pattern is altered but still very different from any of species of *Oropeza.* The green coloration of the abdominal segments and to some extent the zig-zag dorsal markings are carried over from the larva. The leg sheaths, wing pads, thorax and head pass through shades of tan and brown, eventually becoming nearly black, shortly before emergence of the adult. The cast pupal skin often shows an irregular, marbled pattern of dark brown in the region of the thoracic dorsum; this pattern does not show clearly in the older pupa, although it can be made out when the thorax is paler in color. Morphological characteristics of the pupa of *americana* which distinguish it from pupae of species of *Oropeza* are covered in the section on pupal morphology.

Notes on distribution.—Alaska—58 miles southeast of Fairbanks (Alaska Highway Milepost 1465), 10 July. Alberta—Banff National Park, Banff, 4 July; 39 miles south-southeast of Valley View, 10 July. Connecticut—Hartford County, 8 to 12 June; Litchfield County, 9 to 12 June; Tolland County, 14 June. Georgia—Bibb County, 9 June; DeKalb County, 19 August; Fulton County, 25 August to 3 September; Lumpkin County, 23 May; Union County, 10 to 28 June. Illinois—Pope County, 14-15 July. Indiana—Jefferson County, 22 July to 27 August; Jennings County, 3 August; Parke County, 10 to 25 June, 15 July, and 11 to 30 August. Iowa—Boone County, 26 May. Kentucky—Letcher County, 3 July. Labrador—Rigolet, 16 July. Maine—Cumberland County, 1 July; Hancock County, 16 June; Oxford County, 11 July; Penobscot County, 14 June. Maryland—Garrett County, 26 June. Massa-

CHUSETTS—Berkshire County, 13 to 20 June and 19 July; Middlesex County, 11 July; Norfolk County, 11 June; Suffolk County, 11 July. MICHIGAN—Cheboygan County, 2 July; Eaton County, 31 May; Keweenaw County, 25 June; Livingston County, 30 May; Marquette County, 16 July; Oscoda County, 17 June; Presque Isle County, 29 June; Washtenaw County, 12 June. NEW HAMPSHIRE—Carroll County, 4 July; Cheshire County, 16, 19 June; Coos County, July; Grafton County, 29 June and 8 July; Hillsboro County, no date. NEW JERSEY—Bergen County, 5 July; Essex County, June and July. NEW YORK—Albany County, 18 June; Cattaraugus County, 30 June; Essex County, 19 June; Fulton County, 18 June; Hamilton County, 17 to 23 June; Herkimer County, August; Queens County, 22 June. NORTH CAROLINA—Buncombe County, 30 May; Burke County, 14, 21 June and 1 July; Haywood County, 30 June and 29-30 July; Macon County, 11 June and 23 August to 2 September; Swain County, 11 to 19 June and 9 August; Transylvania County, 10 June; Yancey County, 9 to 15 June. NOVA SCOTIA—Guysborough County, 30 June; Halifax County, 29 June; Inverness County, 3 July; Yarmouth County, 27 June. OHIO—Delaware County, May; Harrison County, 5 August; Hocking County, 20 May to 8 June; Portage County, 25 June and 16 August; Washington County, 19 June. ONTARIO—Kenora District, Sioux Lookout, 6 July; Orillia, 10 June. PENNSYLVANIA—Centre County, 25 June and 5 July; Columbia County, 15 July; Luzerne County, 4, 11 to 19, and 27 June and 5 to 10 July. QUEBEC—Bradore Bay (north shore St. Lawrence River), 13 July; Gaspé Peninsula (Mt. Lyell and north shore), 3 July; Knowlton, 26 June. SOUTH CAROLINA—Greenville County, 10 June and 16 July to 30 August; Pickens County, 29 June. SOUTH DAKOTA—Custer County (Harney Peak), 12-13 and 24 July; Pennington County (Horsethief Lake, in Black Hills), 16 and 24 July. TENNESSEE—Blount County, 12 June; Cumberland County, 25 June; Fentress County, 30 May to 24 June, and July and August without dates; Sevier County, 7 May to 13 June, 30 June and 16 September; Scott County, 30 May and 24 July. VERMONT—Chittenden County, 15 to 24 June; Washington County, July. VIRGINIA—Giles County, 5 June to 13 July and 11 to 28 August; Nelson County, 14 August; Rockingham County, 6 July; Smyth County, 20 June; Washington County, 18 August; Wise County, 2 July and 16 August. WEST VIRGINIA—Marion County, 5 August; Pocahontas County, 23 June and 5 July; Preston County, 25 June; Randolph County, 5 July; Tucker County, 24, 25 June; Wetzel County, 5 August.

Dolichopeza (*Dolichopeza*) *borealis*, new species

The following description is based upon a single female, pinned. The specific name refers to the far northern range of the species.

Description.—General coloration dark grayish brown, similar to that of *americana.* Prescutum uniformly dark, without indication of stripes. Scutellum grayish buff as in *americana* but postscutellum dark, not pale as in *americana.* Anepisternum and pre-episternum of mesothorax evenly darkened throughout; that is, without the central pale area found in *americana.* Eyes black. Antennae thirteen-segmented, the terminal segment elongate, about half as long as the penultimate segment; scape and pedicel pale, the flagellum dusky. Wings strongly tinged with grayish brown, the stigmal spot and heavier veins very dark brown. Femora and tibiae dark grayish brown. Approximately the apical one-sixth of each basitarsus is pale, the remainder similar in color to the tibia; the second tarsal segment is pale, white in the hind tarsi but only pale tan to yellowish white (as in *venosa* or *australis*) in the fore and middle tarsi; the third segment darkening and the fourth and fifth very dark, like the legs; claws simple. Abdomen dark grayish brown, lacking distinct annulations. The tenth tergum is strongly sclerotized, its surface glossy. Cerci narrowed in apical one-third and darkened at their tips (Fig. 136); the hypovalves taper rather evenly to a slender tip, instead of being truncate with a projecting apical tooth as in *americana.* Body length of holotype female 15.0 mm.; wing 12.9 mm.

Type.—Holotype female; about 30 miles north of Seward, Kenai Peninsula, Alaska (60°31'N, 149°32'W), 30 June 1957, George W. Byers (Field Catalogue Number 22); in the Snow Entomological Museum, University of Kansas, Lawrence, Kansas.

Descriptive comments.—It is anticipated that discovery of the male of this species will provide additional characters to separate it from *Dolichopeza americana.* At present, the larger size of *borealis*, its peculiar tarsal coloration (which is presumed to be the same in both sexes), and details of structure of the ovipositor will serve to distinguish the two species.

The tarsi in *borealis* are proportionately shorter than in most species of the genus. Thus, while the tarsi of *americana* exceed the combined lengths of femur and tibia, those of *borealis* (assuming the type is representative) are noticeably shorter, as shown in Table 4.

TABLE 4.—Measurements of Leg Segments in *Dolichopeza* (*D.*) *borealis*
(Measurements in Millimeters)

	Femur	Tibia	Tarsus	(Basitarsus)	Total
Fore leg	6.1	6.0	9.9	(7.2)	22.0
Middle leg	6.6	6.8	9.7	(6.7)	23.1
Hind leg	7.1	7.0	10.0	(7.1)	24.1

Geographical distribution.—*Dolichopeza* (*D.*) *borealis* is so far known only from the type locality on the Kenai Peninsula, and it seems likely that its range does not extend far northward or eastward from there. It may, however, occur in the forested lowlands of southwestern Alaska and, if the shade provided by trees is not a limiting factor in its distribution, in the Aleutian Islands.

Habitats.—The holotype was taken in fairly deep shade at the edge of a clump of spruce trees in a hummocky bog, in which species of *Sphagnum* were the predominant mosses. There was much fallen timber in the bog and a widespread undergrowth of brushy, moose-browsed willow. In the open areas among the willows, grasses, sedges and wild rose were growing in the mosses, and there were scattered, small areas of open water.

Seasonal distribution.—The collection date in late June makes it difficult to say whether there are one or two annual generations, but on the basis of knowledge of the other species of the genus it seems reasonable to expect only one summer generation at the latitude of the type locality.

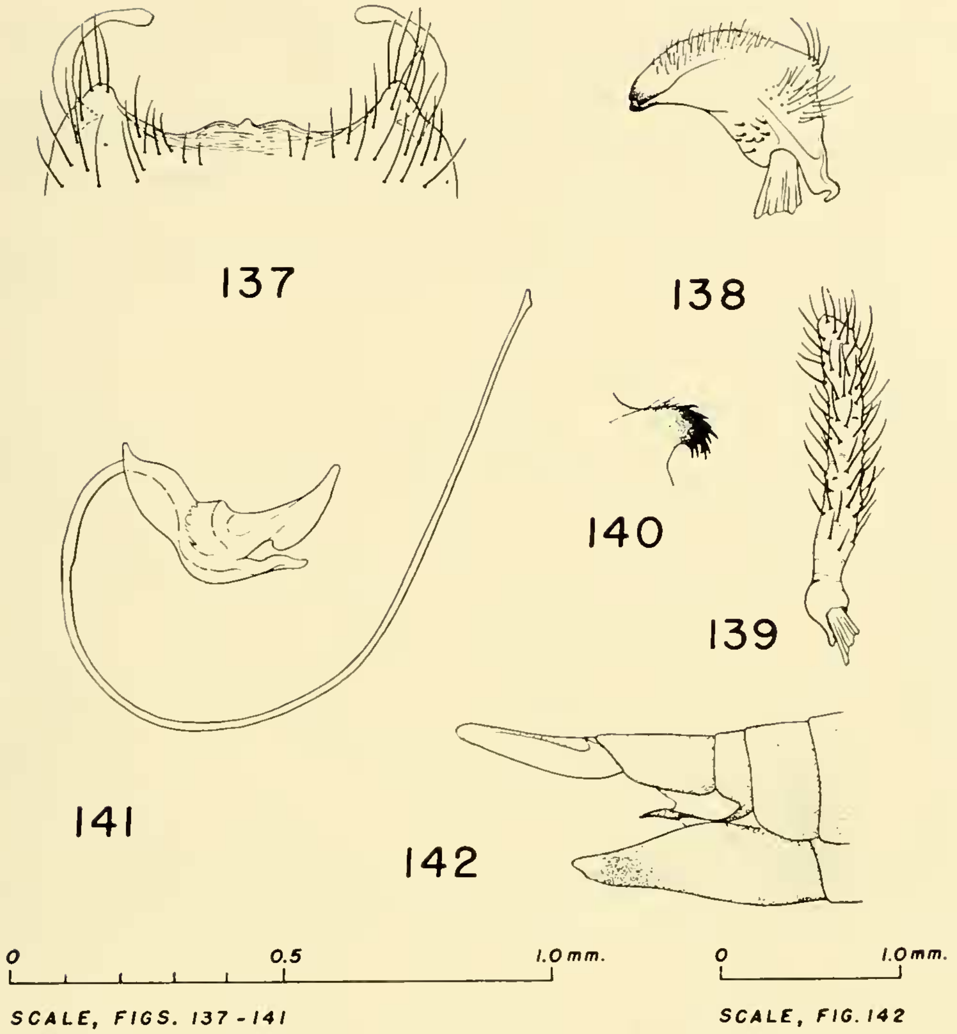
Immature stages.—None of the immature stages of this species is so far known.

Subgenus *Oropeza*

Dolichopeza (*Oropeza*) *australis*, new species

Among specimens of *Dolichopeza subalbipes* from various localities on the southeastern coastal plain, I have found several flies resembling that species in some respects but differing in details of coloration and structure. The following description is based upon 22 males and eight females from Georgia (type series) and two males and two females from other areas. The specific name refers to the fact that this species has the southernmost over-all range of any North American *Dolichopeza*.

Description.—General body coloration light brown with dark brown markings, the tarsi pale. Prescutum dark brown, a pattern of three dark stripes sometimes faintly indicated but usually obscured altogether. (There is, in some specimens, a slightly paler



FIGS. 137-142. *Dolichopeza (Oropeza) australis* new species; 137—ninth tergum of male, 138—left inner dististyle of male, dorsal aspect, 139—left outer dististyle, dorsal aspect, 140—gonapophysis, dorsal aspect, 141—vesica and penis, 142—terminal abdominal segments of female, right lateral aspect.

median line, but I believe this is a post-mortem effect.) Mesothoracic anepisternum brownish, only a little darker than adjacent portion of pre-episternum. Eyes black. Antennae with twelve segments, the scape and pedicel slightly paler than the dusky flagellum. Wings tinged lightly with brown, the stigma darker brown. Femora and tibiae brown, this color extending over approximately the basal two-thirds of each basitarsus and grading through yellowish brown to pale yellowish white on the second through fifth segments. Abdomen light brown with distinct darker brown annulations. The medio-posterior margin of the ninth tergum of the male has a central, pointed tooth with a broader, rounded lobe on either side, the central tooth the longest; and the tergal arms are slender, their tips flattened and slightly widened (Fig. 137). Gonapophyses set with black bristles, as in other species of the *obscura* group. Inner dististyles with an angular protuberance on the outer surface, the elevated area bearing a few strong hairs (Fig. 138). Hypovalves of female ovipositor moderately darkened subapically (Fig. 142). Body length of males is 8.0 mm. to 9.8 mm. (holotype 9.5 mm.); of females 9.8 mm. to 11.6 mm. (allotype 9.8 mm.). Wing length in males varies from 10.4 mm. to 11.8 mm. (holotype 10.9 mm.); in females, from 10.2 mm. to 12.8 mm. (allotype 10.6 mm.).

Types.—Holotype male, Mossy Pond (Emory University Field Station, near Newton), Baker County, Georgia, 27 January 1949, R. E. Bellamy (Catalogue Number 2936). Allotype, same locality and collector, 31 March 1949 (Catalogue Number 3007). Paratypes, 21 males and 7 females from the type locality, as follows: 27 August 1948, 1 ♂; 27 January 1949, 1 ♀, taken in copulation with the holotype but too damaged to be made the allotype; 9 February 1949, 1 ♂; 17 February 1949, 1 ♂, 1 ♀; 24 February 1949, 1 ♂; 24 March 1949, 7 ♂, 4 ♀; 31 March 1949, 6 ♂, 1 ♀; 7 April 1949, 1 ♂, 1 ♀; 21 April 1949, 3 ♂; all collected by Dr. R. E. Bellamy. Holotype, allotype and most of the paratypes are in the University of Michigan Museum of Zoology, Ann Arbor, Michigan; one male paratype has been sent to the United States National Museum, Washington. The few specimens seen from areas other than the type locality have not been designated paratypes.

Descriptive comments.—Dolichopeza australis is most nearly related to *subalbipes* and *johnsonella,* as indicated by the hypopygial structure of the male, especially the inner dististyles and the posterior margin of the ninth tergum. In body coloration, *australis* resembles *johnsonella,* the thoracic pleura lacking the contrast in shade and color along the border between anepisternum and pre-episternum, as found in *subalbipes,* and the prescutum being obscurely marked. However, the coloration of the legs and details of the external reproductive structures of both sexes will easily separate the two species. In *subalbipes,* the tarsi are white and the femora and tibiae are pale with darkened tips, and a part of the last tarsal segment is darker than the remainder of the tarsus. In contrast. the leg segments of *australis* are neither pale nor dark tipped, and the tarsi are pale throughout. The characteristic basal enlargement of the penis in *subalbipes* is only faintly indicated in *australis* (Fig. 141), and details of the external genitalia as well will serve to distinguish these two species. Certain male flies assigned to *subal-*

bipes have slender tergal arms similar to those of *australis,* but the two species may be differentiated by the shape of the margin of the ninth tergum and by the color differences already mentioned.

Of the type series of flies, about one quarter have venational abnormalities in one or both wings. Most of these anomalies consist of absence of a closed cell 1st M_2 (discal cell) by loss of the medial cross-vein.

Geographical distribution.—Dolichopeza australis is so far known from only three localities, one of which is the type locality in southwestern Georgia. The other two, Washington County in southwestern Alabama and Alachua County in northern peninsular Florida, suggest a rather widespread occurrence of the species on the Gulf Coastal Plain. Habitats similar to those in which *australis* has been found also occur in southern Mississippi and Louisiana.

Habitats.—All known habitats of this species are swamps—that is, wooded areas with lush undergrowth and considerable amounts of standing water. Mossy Pond, the type locality, is an isolated cypress swamp of a few acres extent, surrounded by rather dry land that is sparsely wooded with pines. The cypresses are festooned with Spanish moss, while the water below supports a luxuriant growth of floating and emergent vegetation. Mosses growing above the water line on the cypress boles and at the edge of the pond are probably the larval habitat of *australis* and of the other species of *Dolichopeza* (*obscura* and *subalbipes*) found together with it.

Seasonal distribution.—It has been mentioned earlier that in the southernmost part of the range of the genus in North America, *Dolichopeza* seems to reproduce and complete its life cycle as rapidly as local conditions will permit; that is, there is no limitation to one or two annual generations. Date records for *australis* include January, February, March, April and August at the type locality, with the largest numbers having been taken in the last half of March. Records from Alachua County, Florida, are for 12 and 14 November and 16 January, and from Washington County, Alabama, 14 June.

Immature stages.—Eggs of this species average .71 mm. in length and .31 mm. in greatest diameter. They do not have a terminal filament. Larvae and pupae of *australis* have not yet been found, as I have never had the opportunity to study this species in the field. During my brief visit to the type locality, in April, only *Dolichopeza obscura* was collected, and I have never seen even the adults of *australis* alive.

Dolichopeza (*Oropeza*) *carolus* Alexander

Literature references.—*Oropeza albipes* Johnson. Johnson, 1909: 121, pl. 15 (hypopygium); Johnson, 1910: 708; Alexander, 1919: 930; Alexander and McAtee, 1920: 393; Dietz, 1921: 259; Alexander, 1924: 60; Alexander, 1925: 172; Johnson, 1925: 32; Pierre, 1926: 11; Leonard, 1928: 698; Alexander, 1929a: 236; Alexander, 1929c: 297; Alexander, 1930c: 113; Rogers, 1930: 22; Rogers, 1933: 48.

Dolichopeza (*Oropeza*) *carolus* Alexander, new name for *Oropeza albipes* Johnson, preoccupied in *Dolichopeza* by *D. albipes* (Ström). Alexander, 1940: 618; Alexander, 1941a: 295; Alexander, 1942: 211-212, fig. 26A (hypopygium); Whittaker, 1952: 32; Foote, 1956: 221.

Original description.—"Face yellow, rostrum and vertex brown, palpi brown. Antennae yellow, the three basal joints lighter than the others. Thorax dark brown, showing three rather distinct stripes; plurae, scutellum, and metanotum light yellow, translucent, with livid spots below the base of the wings, between the coxae, at the base of the halteres, and on the posterior margin of the metanotum. Abdomen yellow, the black bands connected on the dorsal line leaving a row of large spots on the sides as in *O. venosa*. In the female the bands are more distinct. Genitalia yellow, appendages light yellow, very short or rudimentary, style red, base black, appendages at base of style short and tipped with a slightly curved spine, ventral margin deeply emarginate. Ovipositor reddish brown. Femora yellow, tibiae and tarsi white, tipped with brown. Halteres white, knobs brown. Wings brownish hyaline, veins light brown, stigma dark brown, median cubital cross-vein * present or wanting. Length, male, 10 mm.; female, 13 mm."

Types.—Holotype male, Cohasset (Norfolk County), Massachusetts, 1 July 1907, Owen Bryant. Allotype, Dummerston (Windham County), Vermont, 14 July 1908, C. W. Johnson. Paratypes, six males and four females, together with holotype and allotype in the collection of the Museum of Comparative Zoology, Harvard University; one male and one female in the Academy of Natural Sciences of Philadelphia; and one male in the Alexander collection, at Amherst, Massachusetts. Johnson mentions having twenty-two specimens; however, it is possible that he did not make types of all of them.

Diagnostic characteristics.—Among the species of *Oropeza* in North America, only two possess white tarsi and pale legs, with the tips of femora and tibiae darkened. These are *carolus* and

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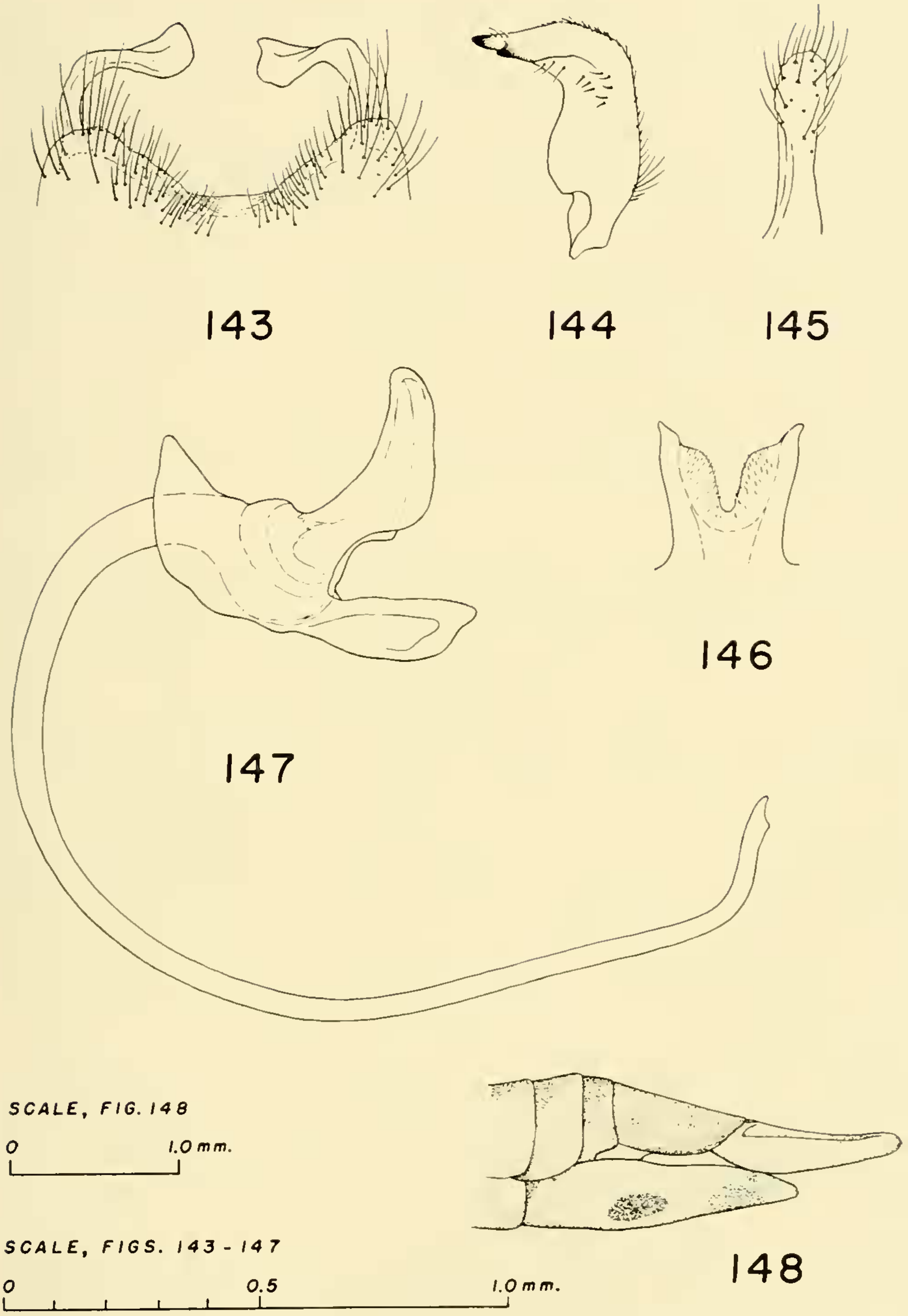
* See page 710.



FIGS. 143-148. *Dolichopeza (Oropeza) carolus;* 143—ninth tergum of male, 144—left inner dististyle of male, dorsal aspect, 145—left outer dististyle, dorsal aspect, 146—gonapophyses, dorsal aspect, 147—vesica and penis, 148—terminal abdominal segments of female, left lateral aspect.

subalbipes. The similarity of coloration and size in these two species is striking, involving nearly every detail. In the field, habitat is an indication of species identity, *carolus* being more often found in rocky places and moist to mesic forests and *subalbipes* in wetter woodlands, along stream banks, and in swamps and marshes. Males of *carolus* may be identified with certainty by their short, pale outer dististyles. Females may be separated from those of *subalbipes* by the presence of a dark, well-defined spot on the basal portion of the hypovalve, on each side, approximately below the ninth tergum (Fig. 148). The absence of sharp contrast of color between the mesothoracic anepisternum and preepisternum in *carolus* is also an aid in distinguishing this species from *subalbipes.* All these features are visible to the unaided eye, so that field determination of collected specimens is not difficult.

Descriptive comments.—The similarity of coloration between *carolus* and *subalbipes* extends to virtually every feature except those few enumerated above, but the darker markings are more intense in *subalbipes,* in specimens that are not faded with age. While *carolus* is a fly of contrasting colors, these are, as in all of the genus, usually more subtle than the paint-box assortment indicated in Johnson's description. There is a degree of brown in all the colors, so that in general appearance *carolus* is light tawny with dark brown markings. Against a dark background, the tarsi are pale enough to be called white, without any chance of confusion. Old or sun-faded specimens take on the appearance of *Dolichopeza venosa,* which species is easily recognized in both sexes by the genitalia.

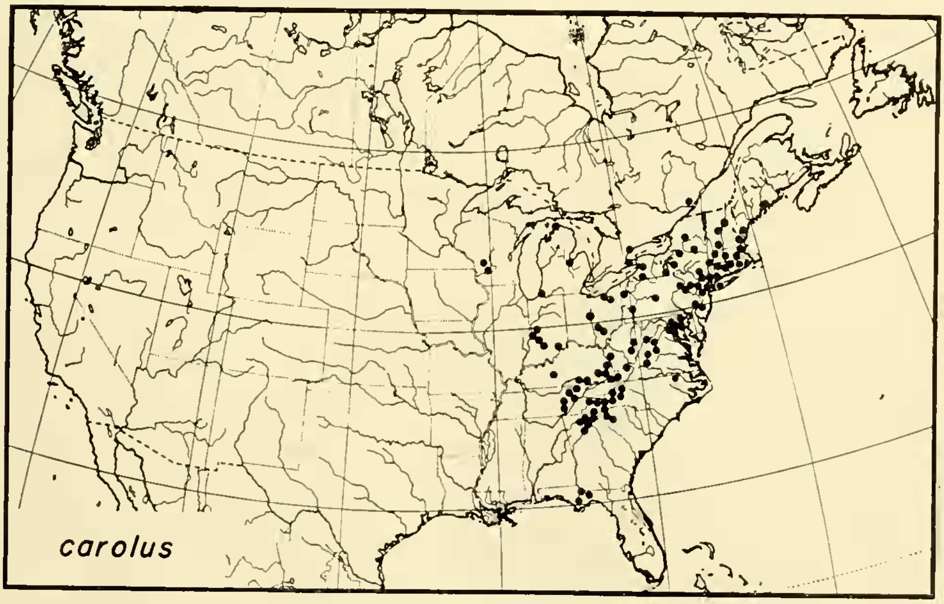
Wing venation in *carolus* deviates only rarely from the subgeneric scheme. An occasional absence of the medial cross-vein or failure of some branch of the media to reach the wing margin are the most commonly seen anomalies. In a collection of 40 males and 20 females from a Georgia locality, only four venational abnormalities were found: one incompletely closed discal cell and three instances of a short spur vein projecting distally from the medial cross-vein. The latter anomaly has also been seen from a few other localities.

Body length of males is from slightly less than 10 mm. to somewhat over 12 mm.; and the wings vary within the same limits. Females measure about 11 to 15 mm., their wings from 10 to 14 mm. The smaller specimens are from August collections, and the larger ones are spring records from Indiana, Michigan and mountainous western Virginia.

Variation in details of the male hypopygium is slight and is found mostly in the shapes of the ends of the tergal arms and of the inner dististyles. The widened, flattened tips of the tergal arms may be elongate, rounded or somewhat pointed, and it is often the case that the two arms of the same fly are unlike (Fig. 143). Curvature of the inner dististyles varies, as does the depth of the apical cleft. It should be mentioned that the apparent shape of such flattened or partially flattened structures as the tergal arms and (in this species) the outer dististyles is considerably affected by a shift in the point of view. Thus, in dorsal aspect (Fig. 145) the outer dististyle seems somewhat narrowed in the basal half, while viewed from the side it is of almost equal width throughout. In the emargination of the ninth tergum and the shape of the tergal arms, *carolus* most nearly resembles *walleyi* and *sayi*, but the gonapophyses are rather like those of *dorsalis*.

The size and configuration of the vesica and its apodemes and the diameter and apical curvature of the penis suggest a relationship of this species with *Dolichopeza venosa* (compare Figs. 147 and 234). The seminal duct in *carolus* is only about one-third as long as that of *polita*, a species of comparable size, and the bases of the accessory glands are enlarged, resembling the common vas deferens at the point where all three ducts enter the seminal vesicle.

Geographical distribution.—The known range of *Dolichopeza carolus* extends from Maine westward to Wisconsin and southward through the Appalachian Mountains. Following cool ravines along



MAP 2. Range of *Dolichopeza (Oropeza) carolus* Alexander. Each spot represents one or more collections within a county (United States) or at a locality.

the Chattahoochee-Apalachicola drainage, *carolus*, apparently an essentially northern species, has reached western Florida, where it is a common member of the tipulid fauna of the Apalachicola River valley, an area unlike the rest of the state. I did not find in the Ozark Mountains what I consider adequate *carolus* habitats, but I would expect to find this species in parts of Minnesota, western Ontario, and other northern areas from which it is not known at this time. There is a published record of the occurrence of this species in New Brunswick (Alexander, 1942: 211), but I have not been able to get more specific data, for which reason the record does not appear on the map.

Habitats.—Adults of *Dolichopeza carolus* are most commonly taken in leafy vegetation, such as is found along small streams through deciduous forests or in rocky ravines where leafy plants and ferns abound. I have never found them far from water or cool shade, although by night or on damp days they may fly a hundred yards or so from their usual streamside haunts. They are numerous in Michigan woodlands in low vegetation in the wetter areas. I found them particularly abundant in the sandstone ravines of Indiana and Ohio, where they rested among ferns and other low plants along the edges of outcropping strata or suspended themselves in the deeper shade of a cranny beneath an outcrop. Following small brooks upstream, I encountered *carolus* nearly as far as there were trees providing shade. Dietz (1921) records *carolus* as ". . . common, June and July, in damp, open woods." On the Cumberland Plateau, Rogers (1930) found them ". . . equally characteristic of wet 'rock-houses,' of the shaded base of dripping cliffs, of upland stream-margin thickets, and of the mossy banks of shaded brooks." In the Florida area mentioned earlier, *carolus* was found in ". . . moist recesses beneath overhanging banks and within rank herbage on shaded stream banks" (Rogers, 1933). Foote (1956) records the species from moist woodland ravines and wet cliff faces.

I have taken *carolus* together with *subalbipes* in deep grasses and broad-leafed weeds along a stream in Virginia, among ferns along a mountain brook in Maine and in a swamp in Wisconsin. In the brushy margin of a mountain bog in Pennsylvania, I took it together with *venosa*, while along a rocky brook course a mile down the mountain it was found together with *americana*. It is my belief that the species does not range far from its larval habitats, which are wet or damp mosses usually occurring near small streams. On one occasion, however, several teneral flies were captured on a mossy but not wet cliff face at 6:30 in the evening, but when I returned to the same spot an hour after nightfall, these and many other adults seen earlier were nowhere to be found.

Seasonal distribution.—From southern Michigan and New England to Georgia, *carolus* seems to have two main periods of emergence annually: one in late May and June, the other in late July through August, the period in any case governed in part by the local weather conditions. Nearly all western Florida records are for March and April, although later summer months are represented. In Michigan and in Wisconsin, *carolus* is on the wing throughout July but mostly early in the month. In Turkey Run State Park, Parke County, Indiana, in 1953, the first individuals of *carolus* were observed on 1 June, two weeks after the start of the emergence of *americana* and nine days after *polita* first appeared. Only a few females were found as late as 10 July, although one mating pair was collected on 12 July. In Neel Gap, Union County, Georgia, in 1952, *carolus* had reached peak emergence on 28 June. Six years later, at the same place, equivalent numbers were found on 10 June.

Immature stages.—Eggs of this species are comparatively wide for their length, measuring around .79 mm. long and .37 mm. wide. Not many more than a hundred eggs appear to be matured and laid by one female. Eggs laid on 15 June, in Indiana, hatched nine days later at outdoor temperatures. In connection with oviposition, there is an interesting observation to relate: while all other species of *Dolichopeza* induced to lay eggs in captivity laid them on or near wet paper pads in the bottoms of the breeding jars, all females of *carolus* (several individuals, in two years) deposited their eggs upon the sides of the glass jars, as if avoiding the paper. Now, if the tip of the ovipositor is sensitive to the appropriate larval environment (see account of oviposition), then this peculiar behavior may have some bearing on the kind of habitat in which the eggs are laid under natural conditions.

The first instar larvae cannot be distinguished from those of other species, at this time, and I have not succeeded in rearing them to the later instars or in locating the latter in their natural habitats. I would expect the larvae of *carolus* to resemble rather closely those of *subalbipes* and *venosa*. Not until the summer of 1958 was I able to find pupae of this species, and I hasten to add that these have been identified only by inference, on the basis of comparison with known pupae and by close association with adult flies. At a Pennsylvania locality, in a season when adults of *americana* and *carolus* only were present, both male and female pupal skins of a species of *Oropeza* were found projecting from mats of the mosses *Tetraphis pellucida* and *Leucobryum glaucum*. The mosses were growing on root-bound soil on the bank of a small brook below a spring. Beneath wood ferns and low broad-leafed plants only a few inches from the pupal site, adults of *carolus* were resting. The pupae most nearly resembled those of *subalbipes* but appeared to belong to a species of the *sayi* group—a combination one would almost expect on the basis of the adults. Their size, the configuration of their spiracular yokes, and other characters (see key to pupae, page 773) make it virtually certain that these are the pupae of *carolus*.

Notes on distribution.—CONNECTICUT—Fairfield County, 23 August; Hartford County, 8 June and 9 July; Litchfield County, 9 July and 23 July to 12 September; Windham County, 30 June. FLORIDA—Gadsden County, 19 April; Leon County, 16 March to 25 May; Liberty County, 27 March to 26 April and 15 to 27 July. GEORGIA—Dawson County, 9 to 27 June; Hall County, 6 June; Lumpkin County, 8 June; Rabun County, 20 May to 12 June and 20 August; Union County, 10 and 28 June. INDIANA—Jefferson County, 3 June and 23 August; Monroe County, 23 June; Montgomery County, 28 June; Owen County, 18 to 27 June; Parke County, 9 June to 15 July and 30 August. KENTUCKY—Bell County, 18-19 June; Edmonson County, June (?); Letcher County, 3 July; Pike County, 3 July; Whitley County, 24 June. MAINE—Hancock County, July; York County, 1 July. MARYLAND—Baltimore County, 17 June; District of Columbia, 30 May and 25 August; Montgomery County, 4 to 15 June, July, and 29 August to 5 September; Prince George's County, 29 June. MASSACHUSETTS—Berkshire County, 12 to 30 June; Hampshire County, 14 July and 9 August; Middlesex County, 7 June; Norfolk County, 1 and 10 July. MICHIGAN—Berrien County, 8 to 17 July; Cheboygan County, July; Saginaw County, 6 June. NEW HAMPSHIRE—Grafton County, 4 July; Rockingham County, no date. NEW JERSEY—Bergen County, 21 June; Burlington County, 3 to 11 August; Morris County, 17 June; Warren County, 11 July. NEW YORK—Cattaraugus County, 4 July; Columbia County, mid-August; Cortland County, 20 July; Erie County, 3 to 10 July; Fulton County, 28 June; Herkimer County, 20 June; Oneida County, July; Orange County, 25 June to 28 July and 27-28 August; Suffolk County, 25 June and 9 August; Tompkins County, 14 July; Ulster County, 28 June; Westchester County, 9 June. NORTH CAROLINA—

Avery County, 14 June; Buncombe County, 15 June; Burke County, 14 June and 9 July; Haywood County, 27 July to 2 August; Macon County, 8 to 22 June; McDowell County, 13 June; Northhampton County, 7 June; Transylvania County, 9-10 June; Yancey County, 10-11 and 22 June. OHIO—Cuyahoga County, 24 June; Delaware County, June; Fairfield County, 8 June; Hocking County, 30 May and 6 to 8 June; Portage County, 24-25 June and 14 July. ONTARIO—Jordan (near Niagara Falls), 1 August; Toronto, 4 July. PENNSYLVANIA—Allegheny County, 14 June; Carbon County, 3 July; Centre County, 13 and 25 June, 2 to 9 July and 5 August; Luzerne County, 13 to 27 June and 5 to 24 July; Mercer County, 25 June; Monroe County, 6 August; Philadelphia County, 31 July, 2 August and 2 September. QUEBEC—Montreal, June. RHODE ISLAND—Kent County, 21 June. SOUTH CAROLINA—Greenville County, 7 June and 1 September; Pickens County, 29 June. TENNESSEE—Bledsoe County, 26 June; Cumberland County, 25 June; Fentress County, 6 June to 16 July and 16 August; Morgan County, 12 June and 5 August; Scott County, 28 to 30 May; Sevier County 10 to 12 and 30 June. VERMONT—Orange County, 11 July; Windham County, 14-15 July. VIRGINIA—Arlington County, 6 June to 4 July and 11 to 25 August; Augusta County, 28 June; Bedford County (locality uncertain), 30 June; Fairfax County, 29 May to 9 June, 11 to 25 July, and 22 August to 5 September; Giles County, 3 June to 13 July and 24 July to 29 August; Rockingham County, 6 July; Shenandoah National Park, 6 July; Smyth County, 20 June; Washington County, 2 July; Wise County, 2 July. WEST VIRGINIA—Mingo County, 3 July; Pendleton County, 26 June; Pocahontas County, 5 July and 7 August; Randolph County, 5 July. WISCONSIN—Juneau County, 6 July; Sauk County, 5 July.

Dolichopeza (*Oropeza*) *dorsalis* (Johnson)

Literature references.—Oropeza dorsalis Johnson. Johnson, 1909: 119-120, pl. 15 (hypopygium); Alexander, 1919: 930; Alexander and McAtee, 1920: 393 (possibly misidentified); Johnson, 1925: 33; Pierre, 1926: 11; Alexander, 1928: 57, Alexander, 1931a: 138.

Oropeza rogersi Alexander. Alexander, 1922a: 6-7; Pierre, 1926: 12.

Oropeza dorsalis rogersi Alexander. Rogers, 1933: 49.

Dolichopeza (*Oropeza*) *dorsalis* (Johnson). Alexander, 1941a: 295; Alexander, 1942: 212, fig. 26B (hypopygium); Rogers, 1942: 59.

Dolichopeza (*Oropeza*) *sessilis* Alexander. Alexander, 1941a: 296-297, fig. 1 (wing) (new synonymy).

Dolichopeza (*Oropeza*) *dorsalis rogersi* (Alexander). Alexander, 1942: 212 (new synonymy).

Original description.—"Face yellow, rostrum and vertex dark brown, palpi blackish; antennae with three basal joints yellow, the remainder fuscous. Thorax dark brown, the three stripes indistinct, the brown extending over the scutellum and metanotum as a broad stripe, leaving only a narrow lateral margin of yellow; pleurae yellowish white, subtranslucent. Abdomen yellow with a dorsal stripe of brown, spreading over the third to the seventh segments and somewhat obscuring the black bands. Genitalia yellowish, appendages black, style short, ventral margin deeply emarginate. Ovipositor brown. Halteres yellow, knobs dark brown. Legs brown, coxae and basal portion of the femora yellow. Wings light smoky brown, veins and stigma slightly darker, the petiole between the discal and second posterior cell very short, the median cubital cross-vein* present. Length, male, 9 mm.; female, 10.5 mm."

Types.—Holotype male, Capens (on Deer Island, Moosehead Lake, Piscataquis County), Maine, 14 July 1907, C. W. Johnson. Allotype, same locality and collector, 15 July 1907. Both are in the collection of the Museum of Comparative Zoology at Harvard University.

Diagnostic characteristics.—The contrasting dark dorsum and pale sides and underparts of the thorax of *dorsalis* make it readily identifiable on sight, both in the field and laboratory, sight recognition being easier, however, when the fly is alive, the contrast then seeming greater. In its natural habitat, this species is most likely to be confused with *Dolichopeza walleyi* or *sayi*, which often occur together with it. From *sayi*, it differs in details of the external reproductive structures in both sexes and in coloration, especially of the thoracic pleura, pale in *dorsalis* and darkly colored on the anepisternum and ventral pre-episternum in *sayi*. Preserved specimens closely resemble the form of *walleyi* that has pale thoracic pleura, particularly if the prescutal stripes are at all distinct. Males of these two species are easily differentiated by hypopygial characters. The faintness of abdominal annulations and the shorter, more heavily sclerotized cerci of females of *dorsalis* will aid in distinguishing them from *walleyi* females having pale pleura, generally yellowish coloration, and the stigmal spot of the wing not deeply colored. Also, the knobs of the halteres are very dark gray-brown in *dorsalis* but are only slightly infuscated in *walleyi*.

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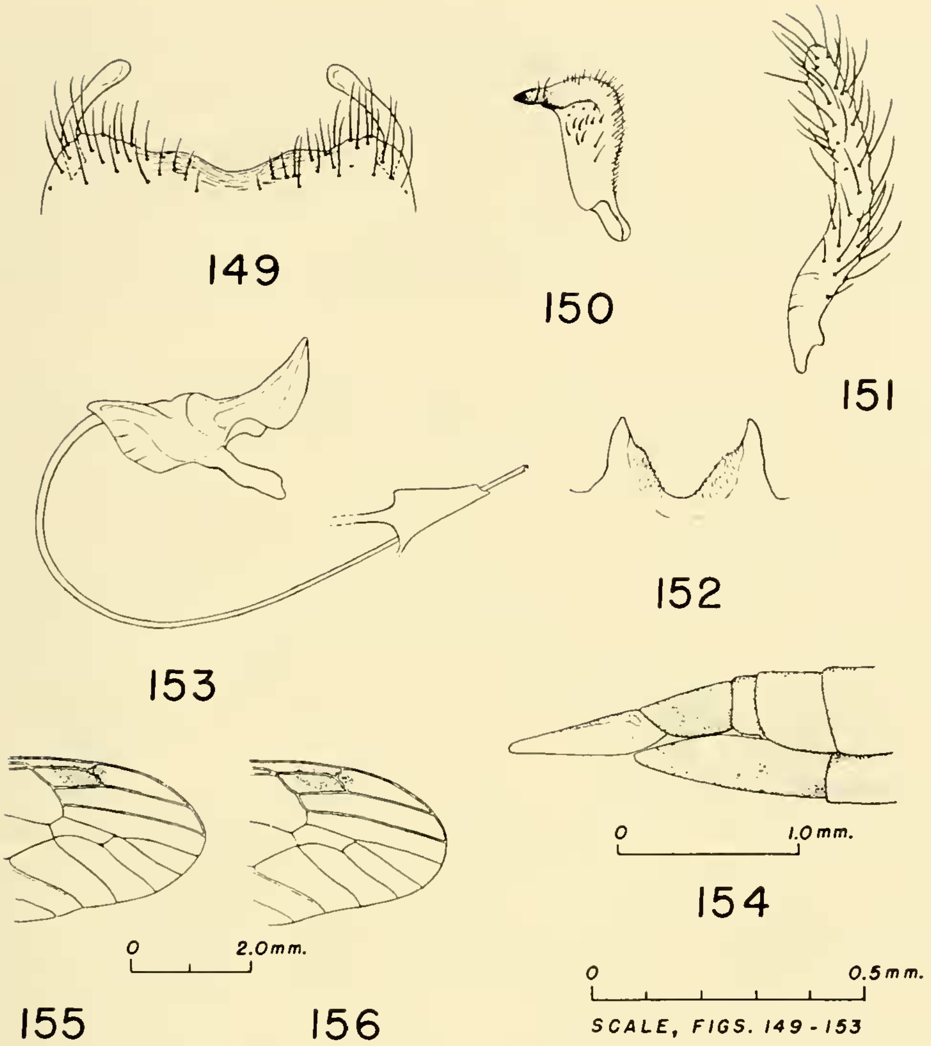
* See page 710.



Figs. 149-156. *Dolichopeza (Oropeza) dorsalis;* 149—ninth tergum of male, 150—left inner dististyle of male, dorsal aspect, 151—left outer dististyle, dorsal aspect, 152—gonapophyses, dorsal aspect, 153—vesica, penis and adminiculum, left lateral aspect, 154—terminal abdominal segments of female, right lateral aspect, 155—apex of wing, showing cell M_1 with short petiole, 156—apex of wing showing sessile cell M_1.

Descriptive comments.—Dolichopeza dorsalis is a small, tawny-yellow fly with a dark, brownish thoracic dorsum and with amber-tinged wings that are relatively wider for their length than in other North American species of the genus. The coloration of the dorsal sclerites of the thorax varies from a rich cinnamon brown to very dark brown. Females, and less often males, may not have the dark coloration extending uninterruptedly along the abdominal terga, as described by Johnson.

An outstanding and very common variation in wing venation in this species is the shortening of that part of the vein M_{1+2} which forms the petiole of cell M_1, that cell being correspondingly elongated. This is mentioned by Johnson in the original description and again in the description of *Oropeza rogersi* (Alexander, 1922a: 6). In every large sample of a population of *dorsalis*, I have found a few flies in which this petiole was extremely short (as Fig. 155) or absent completely (as Fig. 156). In fact, several individuals have been seen in which the cell M_1 was petiolate in one wing and sessile in the other! In view of this, I have placed *Dolichopeza* (*Oropeza*) *sessilis*, distinguished from *dorsalis* by having the cells M_1 sessile, in synonymy with *D.* (*O.*) *dorsalis*.

Dolichopeza dorsalis is the smallest North American representative of the genus, although some males of *americana* and very rarely of other species will be smaller than the average *dorsalis*. Males range in length from about 7 to 10 mm., most being close to 9 mm. Their wings vary from 8.5 to 11 mm. and usually slightly exceed the length of the body. Females measure 9.5 to 12 mm. in body length and 9 to 11 mm. in length of wing. Throughout the range of the species, quite small individuals may be found. On the basis of certain of these, Alexander (1922a: 6) described *Oropeza rogersi*, which was stated to differ from *dorsalis* only in size. In a later review of the genus, Alexander (1942: 212) regarded this small form as a subspecies of *dorsalis*, having a range from southern Indiana eastward to Virginia and southward to Florida. Rogers, nine years earlier, had also considered *rogersi* a subspecies of *dorsalis* (Rogers, 1933: 49). However, among the specimens available to me there are individuals from Michigan and British Columbia that are of small enough size to fit the description of the southern race, *rogersi*, while many specimens from within the described range of *rogersi*, including some from the type locality, are as large as any northern *dorsalis*. Because of this situation, I consider *Dolichopeza* (*Oropeza*) *dorsalis rogersi* a synonym of *dorsalis*.

In its general profile, the ninth tergum of the male of *dorsalis* suggests that of *johnsonella*, although the lateral shoulders are less prominent and the tergal arms are proportionately shorter and more rounded at the tips (Fig. 149). The inner dististyles (Fig. 150) are more like those of *walleyi* or *sayi*, while the gonapophyses most nearly resemble those of *carolus* (Fig. 152). The edge of the gonapophysis that bears the smooth, spinous tip may be dorsolateral in position or may be slightly rotated into a dorsal position. The outer dististyles are very dark brown, except at their bases, which are pale like the rest of the hypopygium. The adminiculum is short, conical and strongly sclerotized.

Except for the venational variation already mentioned, the wings show few departures from the subgeneric pattern. A small closed cell at the distal end of the discal cell connecting it with the cell M_1 has been seen once.

Dolichopeza dorsalis rests with wings outspread and tilted slightly forward. I have noticed that this species sometimes, instead of hanging from overhead support, stands upon vegetation, especially the bent-over leaves of grass. It is a very alert fly, which takes to the wing at the slightest alarm.

Geographical distribution.—*Dolichopeza dorsalis* is the second most widespread member of its genus in the world. Apparently without subspeciation, it ranges across three thousand miles of North America, from Florida and New England northwestward to the Yukon. Its distribution within this vast area (see map) is very poorly known, and extensive further collecting is necessary, especially in the provinces of Canada and the middle Atlantic states, to bridge existing gaps in the range. Only recently (summer of 1959) this species was discovered in an apparently isolated habi-

MAP 3. Range of *Dolichopeza (Oropeza) dorsalis* (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

tat in the Black Hills of southwestern South Dakota. Its occurrence there is discussed more fully in the conclusions.

Habitats.—This species is usually found associated with bogs, swamps and brushy marsh borders. In Michigan, *dorsalis* is "common in shrub and shrub-sedge marshes and near the shrub bordered margins of the sedge-fern-grass marshes. Numerous but local . . . in a variety of other shaded wet situations: tamarack-sumac swamps, birch-maple swamps, and shaded seepage areas" (Rogers, 1942: 59). The holotype of *Dolichopeza sessilis* was collected ". . . in a small accessory swampy patch just off the main stream. . . ." at 2200 feet elevation, in the Great Smoky Mountains, North Carolina (Alexander, 1941a: 296). Rogers (1933: 49) reports *dorsalis* collected in "rank herbage of swampy or marshy rills," in Jackson and Liberty counties, western Florida. The South Dakota habitat was a marsh of grasses, *Carex* spp., *Osmunda* fern, low willow brush, etc., below a spring—a habitat similar in many details to places in which I have collected *dorsalis* in Michigan, Minnesota and elsewhere. *Dolichopeza sayi* often occurs together with *dorsalis* in such environments, but in the Black Hills that species was replaced by the dark form of *walleyi*.

Seasonal distribution.—There is evidence of two annual generations in the collection records from southern Michigan, southern Indiana and North Carolina. Most of the Florida specimens were taken in April, and all were collected in spring. Further north, the first emergence is in June and the second in August. Rogers (1942: 59) estimated the emergence periods, in Livingston County, Michigan, to be from 4 June to 14 July and from 11 to 30 August, in the years 1936 through 1938. The records for farther north in Michigan and for Minnesota, Ontario, and Manitoba, as well as for South Dakota, are all very late June or July. In these regions, it is probable that there is but one generation per year. It is not clear from the collection records in Alberta and northern British Columbia whether there are one or two generations per year in those areas. The latitude would lead me to expect but one; however, at Liard Hot Springs, northern British Columbia, on 13 June 1957, while enroute to Alaska, I found only males of *dorsalis,* suggesting that the flight period was just beginning. Returning on 8 July, I found only females. If the period of emergence of adults had progressed as rapidly as indicated by these collections, it is possible that a second generation might have been produced before the onset of freezing weather.

Immature stages.—The eggs of *dorsalis* average .76 by .31 mm., which is rather large, considering the size of the adult female. I have no counts of the quantity laid by one female but would estimate the number to be ninety. Larvae began to hatch on 22 July from eggs that had been laid on 12 July, by females taken at Lake Itasca, Clearwater County, Minnesota. The first instar larvae of *dorsalis* are of a more buffy color than are those of the other species.

Larvae of *dorsalis* are bright greenish, like the background color of *americana* larvae. Since the green color is not partly concealed by transverse ridges of microscopic hairs on most of the dorsum, as it is in some other species, the larva has by comparison a rather striking appearance. The greenish color is dulled, however, in the thoracic and eighth abdominal segments, by the presence of microscopic hairs that are so long and dense that they give a "woolly" appearance at high magnifications.

The color of the body of the larva probably results from and changes according to the foods chosen by the larva. To see whether this is the case, I offered leaves of *Sphagnum rubellum*, which are dull red in color, to a larva that had been feeding on a green species of *Sphagnum*, probably *S. palustre*. During the several weeks that both mosses were offered as food, however, the larva never fed on the red moss. *Dolichopeza dorsalis* is the only species the larva of which is known to feed on *Sphagnum*, but it is not limited to that genus, having been taken also in *Amblystegium varium*, and possibly in *Plagiothecium denticulatum* growing together with the *Amblystegium* on the floor of a marsh. From these same mosses were reared *Tipula sulphurea*, *Erioptera uliginosa*, *E. needhami*, *Pseudolimnophila noveboracensis*, and *Dolichopeza sayi*.

The pupa has the structure characteristic of its subgenus, combining with this those details by which it is identified in the key to pupae. The spiracular yoke is illustrated in Figure 115. In the laboratory, the pupal stadium was six days. Thorax and wing sheaths were pale tawny when the pupa was two or three days old but darkened to gray about 36 hours before emergence. About 12 hours prior to emergence of the adult, the entire pupal skin darkened, as observed in other species. Throughout the pupal life, the green coloration persists in the abdominal region. The larva of *dorsalis* does not seem to construct a well-organized burrow for pupation, but the tube is evident enough to allow the cast larval skin to be recovered without much searching.

Notes on distribution.—ALBERTA—Bilby (about 30 miles west of Edmonton), 20 July; Lesser Slave Lake, 21 June. BRITISH COLUMBIA—Liard Hot Springs (milepost 496.5, Alaska Highway), 13 and 25 June and 8 July. CONNECTICUT—New Haven County, 3 and 14 July. FLORIDA—Jackson County, 6 May; Leon County, 31 March to 24 April; Liberty County, 25-26 April. GEORGIA—Hall County, 5-6 June. INDIANA—Jefferson County, 2 to 16 June and 18 to 23 August. MAINE—Hancock County, 11 June to 17 July; Piscataquis County, 14-15 July; Washington County, 25 July. MANITOBA—Aweme (20 miles southeast of Brandon), 25 June; Victoria Beach (southeast shore of Lake Winnipeg), 19 July. MARYLAND—District of Columbia (in error?), 17 May and 30 August. MICHIGAN—Alger County, 29 June; Allegan County, no date; Antrim County, 2 July; Berrien County, 11 July; Cheboygan County, 18 July; Lake County, 8 July; Livingston County, 4 June to 14 July and 11 to 30 August; Roscommon County, 1 July; Washtenaw County, 28 May to 24 June and 23 August. MINNESOTA—Clearwater County, 10-11 July; Ramsey County, 6 July. NEW HAMPSHIRE—Grafton County, 12 July. NORTH CAROLINA—Haywood County, 3 August; Macon County, 11 to 15 June; Swain County, 30 June; Transylvania County, 9 June and 8 September; Yancey County, 26 May and 1 August. NOVA SCOTIA—Halifax County, 26 June. OHIO—Hocking County, 8 June. ONTARIO—Burke Falls, 13 July. QUEBEC—Knowlton, 12-13 July. SOUTH DAKOTA—Pennington County (Black Hills), 11 July. TENNESSEE—Campbell County, 10 June.

Dolichopeza (*Oropeza*) *johnsonella* (Alexander)

Literature references.—As *Tipula annulata* Say. Wiedemann, 1828: 54.

Oropeza johnsonella Alexander. Alexander, 1930b: 279.

Dolichopeza (*Oropeza*) *johnsonella* (Alexander). Alexander, 1941a: 295; Alexander, 1942: 212, fig. 26C (hypopygium).

Original description.—"Size small (wing, male, under 10 mm.); mesonotum reddish brown, the brown praescutal stripes relatively indistinct; halteres dusky; legs pale brown, the tarsi a little paler; male hypopygium with the inner dististyle a flattened blade, the apex subtruncate, on outer margin near base with a small setiferous tubercle; gonapophyses recurved, tipped with acute spines.

"Male. Length about 8 mm.; wing 9.8 mm.

"Frontal prolongation of head and palpi dark brown. Antennae (male) relatively elongate, if bent backward extending to beyond the base of abdomen; scape honey-yellow; first flagellar segment short, the remaining segments passing into brown. Head dark brown.

"Mesonotum reddish brown, the praescutum with three indistinct darker brown stripes. Pleura lighter brown, with vaguely indicated darker areas on anepisternum, ventral sternopleurite and ventral pleurotergite. Halteres dusky, the base of stem yellow. Legs with the coxae yellow, infuscated at base; trochanters yellow; a single (posterior) leg remains, pale brown, the tarsi a trifle paler, more yellowish brown. Wings tinged with brown, the stigma darker brown; veins brown. Venation: Cell M_1 about one-half longer than its petiole.

"Abdominal segments ringed with brown and yellow, the apices of the segments paler than the bases. Male hypopygium with the lateral portions of the tergite produced into conspicuous setiferous shoulders, the intermediate margin very gently crenulate; ventrolateral arms of tergite strongly curved, slender, not expanded outwardly, the apex acute or subacute. Outer dististyle a little longer than the inner dististyle, cylindrical, not dilated at base. Inner dististyle a flattened blade, near base on outer margin with a small tubercle set with conspicuous setae; apex of style subtruncate. Gonapophyses recurved, setiferous, the tips set with several acute spines.

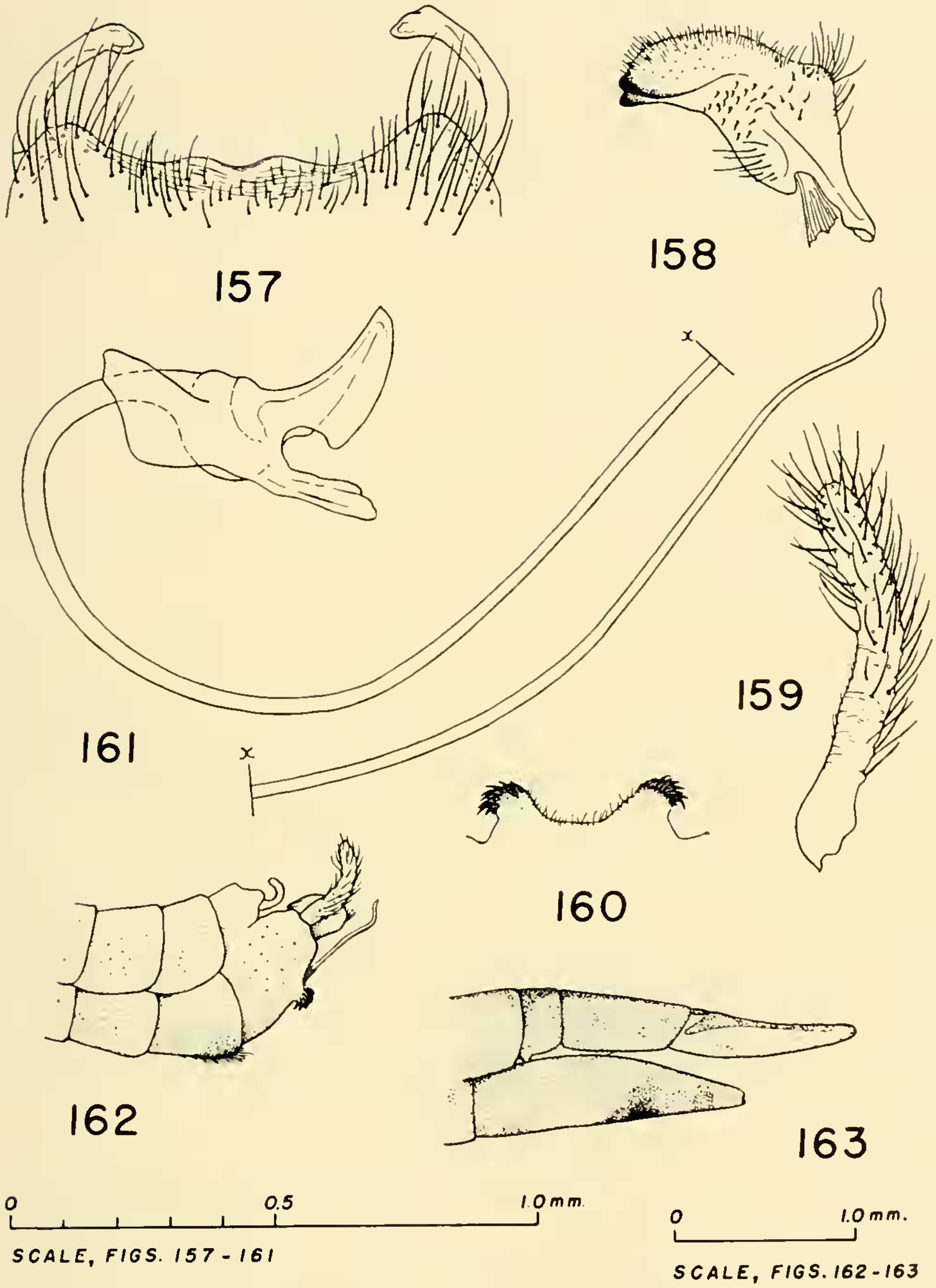
". . . In its small size and general appearance, *Oropeza johnsonella* agrees most closely with *O. rogersi* Alexander, differing in the structure of the male hypopygium, especially the inner dististyle, which bears a setiferous tubercle on outer margin beyond base."

Type.—Holotype male, Riverton (northwest Burlington County), New Jersey, August 1911, C. W. Johnson. This specimen, in the Museum of Comparative Zoology, Harvard University, now consists of the pinned thorax, part of the abdomen, and head with part of one antenna. One broken wing is attached to the thorax. The hypopygium has been mounted in a drop of balsam on a celluloid square attached to the pin; but, due to curling of the celluloid, the balsam has become wrinkled and cracked, as a result of which the hypopygium is scarcely visible and thus worthless. Although the type is of no use for comparison and, in addition, is scarcely typical of the species (as will be explained later), it seems unnecessary at the present to designate a substitute type.

Diagnostic characteristics.—As one of the dusky colored species of the *obscura* group, *johnsonella* is most easily confused with *obscura, polita* and *tridenticulata,* and it is difficult to identify even males without first capturing them. The golden-brown tinge and well-defined, oval stigmal spot of the wing and the presence of discernible stripes on the prescutum and spots on the thoracic pleura all aid in the recognition of this species. A good characteristic for field determination of males is the darkness of the eighth abdominal segment and contrasting paleness of the ninth, especially the sternum, coupled with the presence of a usually conspicuous tuft of black hairs at the ventro-posterior apex of the eighth sternum. This latter feature, overlooked at the time of original description of the species and found only in *johnsonella,* is shown in Figure 162.

Preserved males may be easily distinguished from all other species of the genus by the structure of the hypopygium. Of the *obscura* group, only *johnsonella* and *subalbipes* lack the toothed medio-posterior margin of the ninth tergum. Some specimens of *subalbipes* found in collections were labelled *johnsonella,* and attention was drawn to the white tarsi. Even legless specimens of *subalbipes* of the form having slender tergal arms may be told from *johnsonella* by the fact that the medio-posterior region of the ninth tergum, while it may be only two lobed, is produced caudad, in contrast to the broadly but shallowly emarginate, rather undulating margin of the ninth tergum of *johnsonella* (Fig. 157). Occasionally there is a minute median tooth, suggesting a similarity to *australis;* however, the ninth tergum of the latter has the median tooth projecting beyond the broad lobes. Differences between these two species are discussed more fully under *australis.* Female specimens, sometimes mistaken for faded *Dolichopeza venosa,* are distinguished from that species by the hypovalves: in *venosa,* there is dense sclerotization of the hypovalve from its dorsal margin to the mid-ventral line, beginning beneath about the mid-length of the tenth tergum and extending very nearly to the tip, which is abruptly paler by contrast; in *johnsonella,* the dense sclerotization is more limited to the ventro-lateral surface and is especially intense below the tenth tergum, growing less dense toward the tip of the hypovalve (Fig. 163). Also, even in faded specimens, the golden-brown tinge of the wing will usually still be present and distinguish *johnsonella.* This wing coloration rather resembles that of *similis,* females of which may be recognized by the characters stated in the key.

Descriptive comments.—The original description is fairly adequate as far as coloration is concerned. It might be well, however,



FIGS. 157-163. *Dolichopeza (Oropeza) johnsonella;* 157—ninth tergum of male, 158—left inner dististyle of male, dorsal aspect, 159—left outer dististyle, dorsal aspect, 160—gonapophyses, dorsal aspect, 161—vesica and penis, 162—terminal abdominal segments of male, left lateral aspect, 163—terminal abdominal segments of female, left lateral aspect.

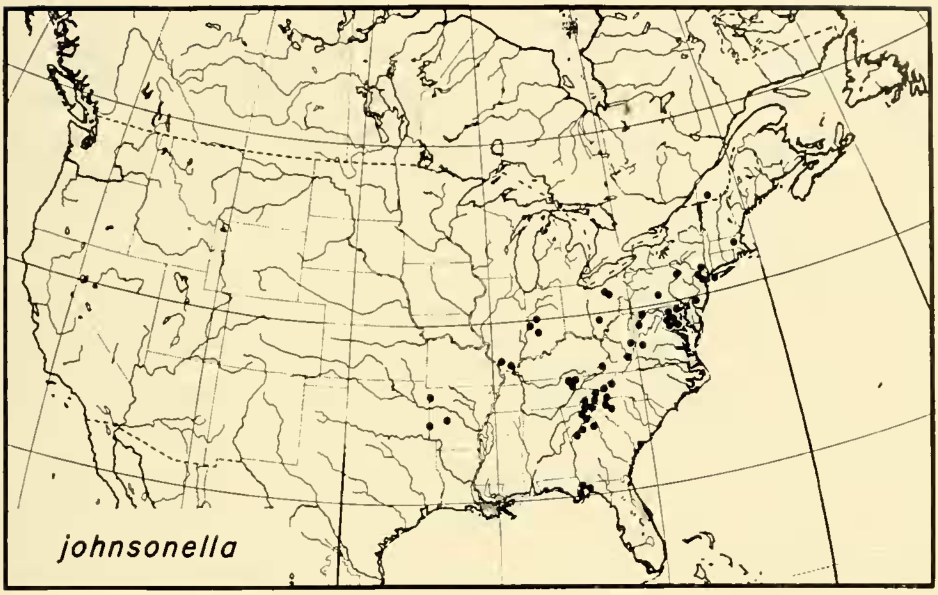
to mention that considerable variation should be expected. For example, prescutal stripes may sometimes be plainly visible, while in other specimens they may be obliterated completely; the legs may be dark brown as well as light brown; and under some conditions of preservation, body coloration of females may be so pale as to cause confusion of this species with *Dolichopeza walleyi,* until close examination of prescutum, wings and abdominal annulation is made.

Venational variations found in *johnsonella* include loss of the proximal half of the vein M_2, presence of Sc_1, presence of an extra cross-vein in cell R_3, branching of M_3 from M_{1+2} beyond the discal cell, loss of the medial cross-vein resulting in absence of a closed discal cell, and presence of a basal fragment of R_{1+2}. All these variations are uncommon, and the venation of the species in general is quite constant. The cell M_1 is not always half again as long as its petiole, as described.

Because the holotype was an autumn fly, affected by environment as described earlier in this report, the size given by Alexander is not precisely characteristic of the species. The fact is that *johnsonella* is one of the larger species of the genus, some females reaching 14 mm. in body length, with wings of equal length. Males measure from 7 to 10 mm., the wing length varying from 9 to 12 mm. In all cases the small individuals were collected in August and September. Females of the late summer generation may be as small as 9 mm. in length, with wings 10 mm. long. The difference in mean size between spring and late summer generations in this species is marked, although individuals as small as the holotype are unusual.

The characteristic structure of the male hypopygium of *johnsonella* has already been described. Variation in the ninth tergum consists of slight differences in breadth of the low, rounded lobes and of the concavity between them, minor differences in length and shape of the tip of the tergal arms, and, as already mentioned, occasional presence of a tiny median projection. The setae on the outer surface of the inner dististyle (Fig. 158) are not always concentrated upon a tubercle (compare Alexander, 1942: 213, fig. 26C) but may be more sparsely distributed over the angular bend of the dististyle.

Geographical distribution.—Previously published records indicate that the range of *Dolichopeza johnsonella* is the Appalachian region from New Jersey to South Carolina, but recent exploration



MAP 4. Range of *Dolichopeza (Oropeza) johnsonella* (Alexander). Each spot represents one or more collections within a county (United States) or at a locality.

has shown that this area is actually only a small part of the species' range. I found it common in three Indiana localities and in smaller numbers in southern Illinois and the Ozark-Ouachita Mountains region, as far west as the Arkansas-Oklahoma border. It also occurs as far north as New England and Quebec. Still, the distribution of this species is only sketchily known. It may be seen, by comparison of the distribution maps of *johnsonella* and other species of the *obscura* group, that the known range of *johnsonella* is very unlike that of any of its near relatives. However, I have seen what I consider appropriate habitats for this species in Missouri, northern Illinois, Wisconsin and Minnesota, and I believe that further collecting will establish that *johnsonella* ranges much more widely than present evidence indicates.

Habitats.—Dolichopeza johnsonella appears to be a denizen of well-shaded situations that are in most cases rocky and often drier than habitats of most species of the genus. In the single published reference to habitats of this species, Alexander (1941a: 295) lists as its haunts in western North Carolina ". . . along Neal's Creek, beneath culverts . . . in small rock caverns below the (Conestee) Falls, associated with *D. (D.) americana* Needham and *D. (O.) dorsalis* (Johnson) . . . along Hughes Ridge trail above Smokemont, 2500 ft., under darkened overhanging banks, swarming in hollows thus formed. . . ." In Indiana, I took *johnsonella* only in shaded crevices or beneath rock outcrops in limestone and sandstone ravines; that is, never in equally dense shade in the woods nearby. My Ohio records are for similar habitats. Collections in the Ozark Mountains and Ouachita Mountains were made along rocky stream beds or on rocky hillsides. In western Florida, the habitats are not rocky but are rather like the piedmont region in many respects, both physically and biologically (Rogers, 1933: 24-25).

Localized aggregations of individuals are sometimes found, as for example along McCormick's Creek, Owen County, Indiana, where I was unable to find *johnsonella* among swarms of resting *Dolichopeza* species for great distances above and below a waterfall, yet beneath certain outcropping ledges of limestone along about a fifty-foot length of the cliff near the fall this species was almost the only one to be found and was present in great numbers. It was this aggregation, incidentally, that led to discovery of a larval habitat for the species. Less pronounced localization of *johnsonella* was noticed at other localities.

Seasonal distribution.—Except in the Florida portion of its range, *johnsonella* has two annual generations, one in June and the other in August. Most Florida specimens were taken in the early days of April. Even the northernmost records seem to represent a June generation, but there have been too few collections of this species in New England and Canada to make this clear. It is my impression, based on concentrated collecting in Indiana, that *johnsonella* reaches its peak of emergence a short while after all other species have passed their peaks. In Pope County, Illinois, in mid-July, it seemed that the local population of *johnsonella* was dwindling at the same time the second generation of *americana* and *polita* was getting underway, but I believe this situation is somewhat atypical for that latitude, especially insofar as the date is concerned. In Indiana, the spring peak of abundance of adults of *johnsonella* comes about the third week of June and the peak of the late summer generation in late August.

Immature stages.—Dissection of gravid females indicates one may lay as many as 120 eggs, which measure, on the average, .74 by .29 mm. These are measurements and counts on June specimens. Eggs laid on the nights of 21 and 22 June began to hatch on the night of 28 June.

In the near vicinity of the concentrations of *johnsonella* described above, the only bryophyte growing in any quantity was the moss *Gymnostomum calcareum.* It therefore seemed likely that this moss was the larval habitat of the crane fly, and a large amount of the moss and its marl substrate was brought into the laboratory and placed in a terrarium. From it, there emerged during the following two weeks or so several adults of *Dolichopeza polita cornuta* and one adult of *johnsonella;* however, as I was away from the laboratory making further collections and field studies, I was unable to find the pupal skin of *johnsonella* at the time of emergence, and it had been destroyed by the time of my return. Thus, while the larval habitat is known, neither late stage larva nor pupa of *johnsonella* has yet been found. Having made a careful examination of the *Gymnostomum* moss before placing it in the terrarium and having found no larvae, I believe they must find daytime shelter in the porous marl deposited by the moss about its lower stems. It will be seen in Table 3 that *johnsonella* has been placed nearer the "dry habitat" end of the scale than would appear warranted on the basis of this one known habitat, which was quite wet. This was done because the species is so often taken as adults in situations where much drier conditions prevail. It is expected that the larva and pupa of *johnsonella* will somewhat resemble *subalbipes,* perhaps having some characteristics of *obscura.*

Notes on distribution.—ARKANSAS—Garland County, 31 July; Polk County, 30 July; Washington County, 30 July. FLORIDA—Gadsden County, 28-29 March; Leon County, 18 March and 16 to 24 April; Liberty County, 3 to 18 April. GEORGIA—De Kalb County, 19 August; Fulton County, 25 August and 24 September; Hall County, 6 June; Lumpkin County, 7 June; Oconee County, 21 August; Rabun County, 12 June; Union County, 10 and 28 June. ILLINOIS—Jackson County, 4 June; Pope County, 14-15 July. INDIANA—Montgomery County, 28 June; Owen County, 8 and 18 to 26 June; Parke County, 10 to 28 June and 30 August. MARYLAND—Baltimore County, 14 to 17 June; District of Columbia, 11 June and 9 July; Garrett County, 26 June; Montgomery County, 7 June and 18 August; Prince George's County, 29 June. MASSACHUSETTS—Middlesex County, 18 June. NEW JERSEY—Bergen County, 1 to 15 June; Burlington County, August; Essex County, June. NEW YORK—Nassau County, 27 June; Orange County, 26 August. NORTH CAROLINA—Cherokee County, 31 August; Haywood County, 29 July; Macon County, 8 to 12 June and 4 to 7 September; Swain County, 20 June; Transylvania County, 8-9 June and 8 September; Yancey County, 6 to 14 June. OHIO—Hocking County, 7 June; Portage County, 25 June; Summit County, 19 June. PENNSYLVANIA

—Huntington County, 9 July; Luzerne County, 10 July. QUEBEC—Knowlton, 20 June. SOUTH CAROLINA—Greenville County, 20 May; Pickens County, 29 June. TENNESSEE—Fentress County, 31 May to 18 June and 11 August to 3 September; Morgan County, 12 June; Scott County, 30 May. VIRGINIA—Arlington County, 11 to 25 August; Augusta County, 28 June; Fairfax County, 30 May, 5 and 16 June, and 30 August to 2 September; Giles County, 11 June to 7 July and 12 August; Wise County, 2 July. WEST VIRGINIA—Pocahontas County, 23 June; Tucker County, 24 June.

Dolichopeza (*Oropeza*) *obscura* (Johnson)

Literature references.—Oropeza obscura Johnson. Johnson, 1909: 122, pl. 15 (hypopygium; wing figured as this species is actually of *tridenticulata*); *Johnson*, 1910: 708; Alexander, 1919: 930, pl. 43 (wing); Alexander, 1920: 983-984, pl. 86 (larva figured is *tridenticulata;* pupa is *polita*); Alexander and McAtee, 1920: 393; Alexander, 1925: 172; Johnson, 1925: 33; Pierre, 1926: 11; Alexander, 1928: 57; Leonard, 1928: 698; Alexander, 1929a: 236; Alexander, 1930a: 272; Alexander, 1930c: 113; Rogers, 1930: 22-23 (includes *polita* and *tridenticulata*); Alexander, 1931a: 138; Dickinson, 1932: 212, Fig. 114 (wing) (apparently refers to *tridenticulata* and *polita pratti* only); Rogers, 1933: 49.

Dolichopeza (*Oropeza*) *obscura* (Johnson). Alexander, 1936: 280; Alexander, 1940: 620; Alexander, 1941a: 295; Alexander, 1942: 212, 214, fig. 26D (hypopygium); Rogers, 1942: 59, 121; Whittaker, 1952: 36.

Dolichopezia (*Oropeza*) *obscura* (Johnson). Rogers, 1949: 12 (typographical error).

Note: *Dolichopeza obscura* Brunetti, 1912, became a secondary homonym of *Oropeza obscura* Johnson, 1909, when the two genera were combined in 1931. Brunetti's species, from India, was also recently placed in the subgenus *Oropeza*, according to Dr. Alexander, who is renaming it.

Original description.—"Head and thorax dark brown, opaque; palpi black, antennae fuscous, the two basal joints yellow; abdomen light brown somewhat shining, the black bands at the incisures not connected on the dorsal line. Genitalia yellowish, appendages blackish; style yellow, long and very slender, curved and often extending to the base of the penultimate segment, appendages at the base of style short and armed with small black spines, margin but slightly emarginate. Ovipositor brown, cerci yellow. Halteres yellow, knobs brown. Legs brownish yellow. Wings smoky brown, the veins and stigma a slightly darker brown, the median cubital cross-vein wanting. Length, male, 8 mm.; female, 10 mm."

Types.—Holotype male, North Adams (Berkshire County), Massachusetts, 19 June 1906, C. W. Johnson. Allotype, Hammond's Pond, near Brookline (Norfolk County), Massachusetts, 18 June 1908. Five male and one female paratypes are together with the holotype and allotype, in the Museum of Comparative Zoology at Harvard University. Of these, the males labelled Auburndale, Massachusetts, 11 July 1905, Squam Lake, New Hampshire, 14 July 1907, Norwich, Vermont, 7 July 1908, and North Adams, Massachusetts, 19 June 1906, are actually *Dolichopeza tridenticulata* Alexander. The allotype and one female paratype may also be this species, but I could not be certain at the time I examined these specimens. Another male and female, both paratypes and both *obscura*, are in the collection of Dr. Alexander, at Amherst, Massachusetts. One male bearing the same label data as the holotype, thus probably one of the original paratypes although not so labelled, is in the Snow Entomoloical Museum, Lawrence, Kansas. Two female paratypes are in the collection of the Academy of Natural Sciences of Philadelphia. Johnson based his description of *obscura* on thirty-four specimens; the present whereabouts of the twenty-one not accounted for here is unknown.

Diagnostic characteristics.—Males of *obscura* may be at once recognized by the shape of the lateral arms of the ninth tergum. In no other species are these structures widely flared apically, then emarginate at the tips (Fig. 164). The profile of the medioposterior margin of the ninth tergum is also a very useful character, having three distinct and rather widely separated teeth, the median tooth usually shorter than the others.

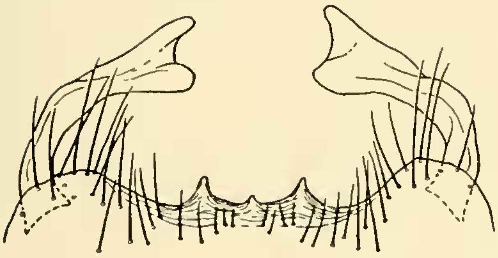
Even after considerable experience with this species in the field, it is difficult and not reliable to make sight identifications. *Dolichopeza obscura* too closely resembles *tridenticulata* for field recognition without capturing specimens. In most places where I have found the two species together, *obscura* has been the more darkly colored, although, particularly in the northern parts of the range, the coloration of both is nearly alike. The same might be said of their relative sizes: *obscura* in most parts of the range is slightly larger than *tridenticulata,* but in the northern states and Canada and at many localities in the highlands of the Appalachians, *tridenticulata* often reaches the size of *obscura.* The wing coloration of *obscura* is more intense than that of *tridenticulata,* but it is almost necessary to see the two species together, knowing which is which, in order to appreciate this comparison.

Female specimens may be distinguished from *polita* by having distinct annulations on the abdomen and the prescutum dark brown and never shining. Lack of stripes on the thoracic dorsum and differences in coloration of the hypovalves of the ovipositor will separate *obscura* from *johnsonella.* Separation of *obscura* and *tridenticulata* females is very difficult. The details of coloration of the hypovalves mentioned in the key to adult females is the most reliable character I have found and is based upon study of a large number of females of known identity, as those taken in copula. A peculiarity noted in many preserved specimens is that while the cerci of *obscura* remain in alignment with the rest of the abdomen, those of *tridenticulata* are often deflected ventrad, so that the tips of the hypovalves are concealed between them. I have not discovered any anatomical reason for this difference of position of the cerci in killed flies. The color differences between *obscura* and *tridenticulata* described for males apply also to females.

Associated males are a help in identifying either *obscura* or *tridenticulata* females, as they provide at least standards for comparison of color. Habitat also, within certain limits, will aid in identification.

Descriptive comments.—Dolichopeza obscura is the darkest of the species of *Oropeza,* a very dusky-brown fly that is nearly invisible in the deeply shaded recesses beneath trees and rocks where it hides by day. The annulated pattern of abdominal coloration is distinct. The occiput of the head is a very dark grayish brown but scarcely darker than the deep brown of the pronotum and prescutum. Johnson's description of the wing coloration as "smoky brown" is apt, for the ground color does indeed suggest smoked glass. The veins and stigmal spot are dark brown, usually contrasting more with the ground color than is the case in *tridenticulata.*

Although irregularities in wing venation are not at all uncommon in *obscura,* I have not found any strong local concentrations of particular variations, such as described earlier for *tridenticulata.* Absence of the medial cross-vein is the most frequently observed abnormality of venation. Loss of sections of veins in the medial field is not unusual, and the presence of the vein Sc_1 has been noted many times. Junction of the m-cu cross-vein near the mid-length



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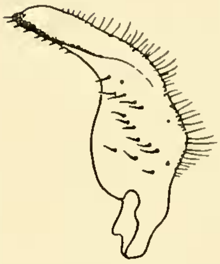

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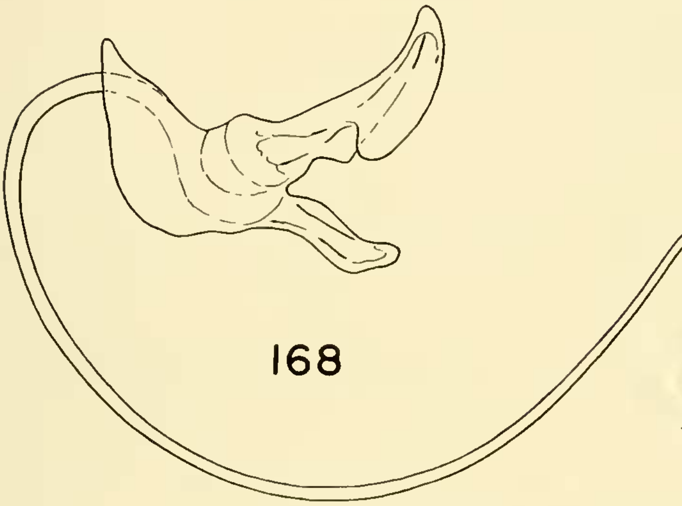

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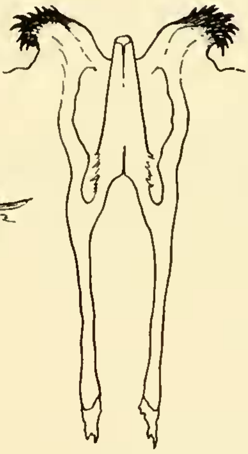

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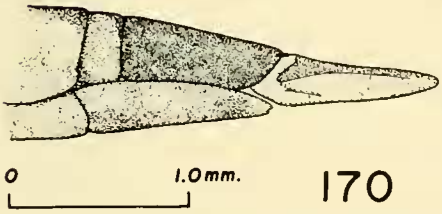

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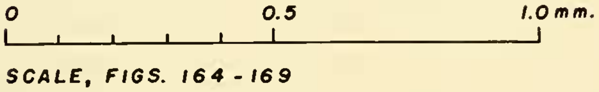


FIGS. 164-170. *Dolichopeza (Oropeza) obscura;* 164—ninth tergum of male, 165—left inner dististyle of male, dorsal aspect, 166—left outer dististyle, dorsal aspect, 167—gonapophyses, adminiculum and adminicular rods, dorsal aspect, 168—vesica and penis, 169—medio-posterior margin of ninth tergum of male holotype, 170—terminal abdominal segments of female, left lateral aspect.

of the short M_{3+4} is quite common. One specimen was seen in which the cell M_1 was very short, its petiole correspondingly elongated, and one other had an extremely short discal cell in both wings. A short spur directed proximally from about mid-length of the m-cu cross-vein has been seen once.

Body length of males varies from 7.5 to 10 mm., the wing length from 9 to 12.5 mm. Females measure from slightly under 10 mm. to 12 mm. in body length, their wings from 10 to 13 mm. Most of the larger specimens I have seen were from the northern states and from high elevations in the central Appalachian Mountains (North Carolina and Virginia), in July and June, respectively. Smaller individuals were found in October and March collections from northern Florida and southern Georgia (Baker County).

Variation in the ninth tergum of the male consists mainly of differences in shape, length and spacing of the three acute teeth of the margin, and of fluctuations in the width, curvature and apical outline of the tergal arms. In the holotype, for example, the central tooth is deflected to one side (Fig. 169); in a specimen from Whitley County, Kentucky, there are four teeth, the usual median tooth apparently having become divided; and in a male from Westmoreland County, Pennsylvania, one of the lateral teeth has an apical bristle, while the central tooth is represented only by a bristle and the entire medio-posterior margin is atypical in form. Breadth of the basal portion of the inner dististyle varies noticeably, although the over-all shape of this structure never approaches that of any other species of *Dolichopeza.* The inner dististyle is narrower, compared to its length, in *obscura* than in the other species (Fig. 165).

In males, the antennal length is nearly equal to half the length of the body. Scape and pedicel are usually of a yellowish gray color, the flagellum darkening from that to deep fuscous at the tip.

Geographical distribution.—Collection records indicate that *obscura* is the commonest *Dolichopeza* in North America. It has been found from Nova Scotia westward to Alberta, southward to Florida and southwestward to Arkansas. I expect it will subsequently be found in swampy areas of Louisiana and Mississippi, in the Ozark Mountains of Missouri and in the rocky ravines of Iowa. The distribution map of this species shows the range fairly well outlined in eastern North America, and although I anticipated *obscura* would occur somewhat westward from Manitoba and Minnesota, I was rather surprised to find it in a forest in western Alberta, in 1957.

MAP 5. Range of *Dolichopeza (Oropeza) obscura* (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

Collections such as this and my earlier discoveries of *obscura* in Kansas and Arkansas serve to emphasize how little still is known of the geographical distribution of many of the North American crane flies.

Habitats.—The relative commonness of *obscura* in collections is very probably a reflection of its ability to flourish in a wide variety of general environments. This is the only species of *Dolichopeza* that seems equally at home in rock gorges, in moist to wet woodlands, and swamps, bogs and border vegetation of marshes. In southern Michigan, Rogers (1942: 59) found *obscura* "numerous to occasionally common in the most densely shaded birch-maple-elm and tamarack-sumac swamps. Numerous but very local in oak-hickory woods, where they were occasionally taken from the dark interior of a hollow stump or log." In his ecological study of the Tipulidae of northern Florida (Rogers, 1933), he records this species as occurring ". . . within hollow trees and dark, cool recesses of banks and cliffs." Habitats of *obscura* on the Cumberland Plateau are described as ". . . shaded, rocky, upper, talus slope brooks, 'rock-houses,' beneath overhanging banks of the upland brooks, and . . . large hollows in standing trees. Rare in the stream-margin thickets" (Rogers, 1930: 23). In central Indiana and Ohio, I found *obscura* in sandstone ravines and rarely in limestone ravines, which seem to be drier, but more often the species was taken in upland woods. In numbers of individuals, *obscura* never equals *polita* or *tridenticulata* in the rock gorge habitats. In northern Michigan, *obscura* is extremely numerous in mesic and wet woodlands, especially in areas of deciduous forest. In the white cedar swamps and drier coniferous forests, it was always found comparatively less abundant. In the spruce forests along the crest of the Appalachians, however, *obscura* is the commonest *Dolichopeza.*

It is my impression that *Dolichopeza obscura* is the most strongly negatively phototropic member of the genus. Where this species was observed resting together with *americana* and *polita cornuta,* in Parke County, Indiana, it was in the darkest recesses of cavities shared by the three species. In other localities, also, *obscura* is found concentrated in the most intense shade available, and the flies are less readily driven from their hiding places than is the case with other species. In view of this reaction to light, it might seem surprising that *obscura* has been more often taken in light traps than any other species of its genus. On the University of Florida Conservation Reserve, at Welaka, Putnam County, Florida, Dr. R. E. Bellamy operated a light trap on most nights of the year 1946, taking six individuals of *Dolichopeza obscura* in April, three in May, seventy-five in June, five in July, two in August, none in September, and seven in October. He also obtained March, September and November records, that year, by other means. The only other *Dolichopeza* Bellamy found was *subalbipes,* which came to the light trap in much smaller numbers. It should be mentioned that Bellamy's light was very near the daytime resting places of the crane flies. It seems likely that *obscura* was present in the vicinity of his trap in great numbers and that because the species is active at night a certain number of flies randomly wandered to the light. It is, of course, possible that the reaction of *Dolichopeza obscura* (as well as other species) to light is like that of many moths, which are repelled by the bright light of the sun by day but are attracted to lights of lower intensity at night. In Cheboygan County, Michigan, I operated a light trap on a dry hill top, a few hundred yards distant from any known diurnal haunts of *obscura,* and still trapped, during July and August, half a dozen specimens. This suggests that *obscura* does not vigorously avoid light under all circumstances.

Seasonal distribution.—There is evidence, locally through much of the range, that there are two generations per year, except in Florida and in the northernmost parts of the range in the United States and Canada. In southern Michigan and in Indiana, I have found two well-marked annual generations, the first from about mid-June to early July and the second from mid-August to early September. In 1953, however, the first male of *obscura* seen at Turkey Run State Park, Parke County, Indiana, appeared on 28 May, about two weeks after the emergence of *americana* began; but there were only one or two individuals of *obscura* observed on any day until 9 June, when an abrupt increase in numbers was noted. There are Florida records for nearly every month of the year, although peaks of abundance occur in March and June. Scattered collection records indicate that *obscura* is present in greater or smaller numbers during June, July and August, in virtually any part of the known range. It is only in areas of concentrated collecting that the two-generation pattern becomes evident. The July-August trend in numbers of individuals and ratio of males to females in the northern Michigan populations suggests that there is only one, generally midsummer generation each year in that area.

Immature stages.—Eggs of *Dolichopeza obscura* from Michigan averaged .73 by .40 mm., which is unusually wide for the length. Smaller females from Florida and Georgia were found to contain shorter eggs which were comparatively more slender, measuring .65 by .28 mm. Duration of the egg stage appears to vary with temperature, for I found it to be about ten days, in northern Michigan, in late July, while Rogers (1933: 32) reports 13 to 16 days, in Florida, in March and April. Based upon dissection of teneral, gravid females, the number of eggs produced by a single fly is close to 120, perhaps occasionally more than that but probably more often fewer, I believe, for that average count includes late-stage unmatured eggs in the ovarioles, which I have reason to suspect may not be matured and laid.

A previously published account of the larva of *obscura* (Alexander, 1920: 983) described the habitat as dry moss, *Hedwigia albicans;* however, in later investigations, Rogers (1933: 49) discovered the immatures of *obscura* in "wet to moderately dry moss clumps; pupation in short tunnels between moss and wood." In my own studies, I repeatedly reared *obscura* from damp mosses, never from dry ones. I then discovered, from morphological studies of the larvae, that Alexander's notes actually applied to *tridenticu-*

lata, which species had then not yet been recognized as distinct from *obscura.* In hardwood swamps in southern Michigan, I found larvae of *obscura* numerous in the moss, *Tetraphis pellucida,* growing on decayed stumps and roots on hummocks; and less commonly they were found in mats of *Heterophyllium haldanianum* moss growing on sodden, rotten logs. Other larval habitats on the low hummocks in swampwoods were the mosses *Hypnum curvifolium* and *Leucobryum glaucum,* the latter growing much more luxuriantly there than it does more commonly on drier soil in upland woods. Although mosses growing on decayed wood are the commonest larval habitats of *obscura* wherever the species occurs, I have also reared it from bryophytes growing on soil, such as the moss, *Fissidens taxifolius,* and the liverwort, *Chiloscyphus pallescens,* both found on glacial till on well-shaded slopes.

The fourth instar larva may be identified by the presence of conspicuous transverse ridges of microscopic hairs on the dorsum of the thoracic and all abdominal segments, with the intervening rows of minute microscopic hairs long, irregular, and with their ends not clearly defined. On a typical abdominal segment, there are from front to rear four ridges about equally spaced, then a wider space, then a fifth well-marked ridge, followed by two or sometimes three fainter, more irregularly spaced ridges. The larva constructs a distinct burrow, in most mosses, in which to pupate.

Pupae of *Dolichopeza obscura* frequently occur together with those of *subalbipes* in a single mat or cushion of moss, and the pupae are very much alike. In both, the pleural spines of the second through seventh abdominal segments bear a single, long bristle, and in both the middle projections of the eighth abdominal sternum are set very close together or upon a common base. The spiracular yoke of *obscura* (Fig. 116) is, however, unlike that of *subalbipes,* as described in the key to pupae. Comparing pupae of the two species during their development, I noted that by the fourth day the pupa of *obscura* had an over-all grayish brown color, the wing sheaths somewhat paler and the thoracic dorsum brown, while the pupa of *subalbipes* was decidedly more greenish—rather a mixture of brown, gray and green difficult of description—the wing sheaths again paler but the thoracic dorsum grayish green.

Notes on distribution.—ALBERTA—39 miles south-southeast of Valley View, 10 July. ARKANSAS—Garland County, 31 July; Washington County, 30 July. CONNECTICUT—Litchfield County, 9 and 23-24 July. FLORIDA—Alachua County, 7 to 29 March, 1 to 25

April, 3 May, 10 June, 4 and 29 July, 16 October and 14 November; Escambia County, 7 April; Gadsden County, 29 March to 19 April; Hernando County, 21 March; Jackson County, 31 March, 12-13 April and 6 May; Leon County, 31 March, 14 to 24 April and 13 June; Liberty County, 27 March and 3 to 13 April; Madison County, 1 September; Marion County, 24 March to 4 April; Putnam County, 26 date records from February to November, with peak abundance in early June; Washington County, 8 June. GEORGIA—Baker County, 19 date records for January through May, July, August and October; Chattahoochee County, 11 October; DeKalb County, 4 October; Lumpkin County, 23 May; Union County, 10 and 28 June; Ware County, 1 July. ILLINOIS—LaSalle County, 7 July; Ogle County, 19 June. INDIANA—Allen County, 10 July; Jefferson County, 7 June and 1 August; Monroe County, 23 June; Montgomery County, 28 June; Parke County, 28 May to 29 June, 15 July and 1 and 30 August. KANSAS—Douglas County, 30 August. KENTUCKY — Barren County, 2 August; Whitley County, 24 June. MAINE—Cumberland County, 1 July; Hancock County, 16 August; Oxford County, 11 July; Piscataquis County, 17 July; Washington County, July. MANITOBA—West Hawk Lake, near Rennie, 4 August. MARYLAND—Baltimore County, 14 and 17 June; District of Columbia, 29 August (reported 17 May to 30 August, but these records are not supported by available specimens); Garrett County, 26 June; Montgomery County, 30 May; Prince George's County, 18 June. MASSACHUSETTS—Berkshire County, 19 June and 10-11 August; Hampden County, 3 August; Norfolk County, no date; Suffolk County, 8 August. MICHIGAN—Antrim County, 2 July; Cheboygan County, 22 June to 8 August; Chippewa County, 13 to 15 July; Emmet County, 20 July to 4 August; Gogebic County, 6 August; Huron County, 20 June; Iosco County, 22 July; Lake County, 22 June to 12 July; Livingston County, 27 May to 9 July, 31 July, and 11 August to 9 September; Mackinac County, 27 July to 7 August; Marquette County, 13 to 17 July; Oceana County, 26 July; Oscoda County, 23 to 26 June; Otsego County, 1 to 4 July; Presque Isle County, 28 July; Washtenaw County, 12 June to 3 July and 10 to 15 August. MINNESOTA—Carlton County, 5-6 August; Hennepin County, 12 June; Winona County, 7 July. NEW BRUNSWICK—Frederickton, 26 August. NEW HAMPSHIRE—Cheshire County, 16 June; Coos County, 2 to 11 July; Grafton County, no date; Merrimack County, July (?). NEW JERSEY—Bergen County, 1 to 15 June; Burlington County, 11 August. NEW YORK—Albany County, 17 June to 3 July; Cattaraugus County, 29 June to 4 July; Chenango

County, 21 July; Cortland County, 20 July; Erie County, 16 June to 10 July; Fulton County, 15 June to 20 August; Greene County, 1 July; Hamilton County, 12 and 30 July; Herkimer County, 3 July and 12 August; Oneida County, 20 June and July; Orange County, 26 to 28 August; Suffolk County, 5 July; Tompkins County, 6 July; Warren County, 26 July. NORTH CAROLINA—Avery County, 14 to 16 June; Buncombe County, 29 May and 13 June; Burke County, 14 June and 1 July; Haywood County, 30 July; Macon County, 8 to 15 and 29 June, and 24 August to 3 September; Mitchell County, 16 June; Swain County, 11 to 30 June; Transylvania County, 8 to 13 June; Yancey County, 26 May, 2 to 22 June and 1 July. NOVA SCOTIA—Guysborough County, 30 June; Victoria County, 1 July. OHIO—Hocking County, 30 May and 7 June; Portage County, 24 June. ONTARIO—Algonquin Park, 23 June to 11 July, and 21 August; Burke Falls, 14 July; Gull Lake, Muskoka District, June; Lake of the Woods, Kenora District, 4 August; Lyn (20 miles northeast of Gananoque), 10 August; Niagara Glen, 30 June; Normandale (on Lake Erie, about 10 miles south of Simcoe), 28 June; Pte. au Baril, Georgian Bay, 6 August; Severn (Lake Simcoe), 16 June; Thunder Bay (Lake Superior), 8 July. PENNSYLVANIA—Bedford County, 8 July; Centre County, 25 June; Columbia County, 15 July; Huntington County, 9 July; Luzerne County, 17 to 28 June, 5 and 10 July and 15 August; Mercer County, 25 June; Sullivan County, 27 June and 10 July; Wayne County, 18 July; Westmoreland County, no date. QUEBEC—Knowlton, 29 June to 12 July; Rigaud, 25 June. RHODE ISLAND—Washington County, 18 June and 10 August. SOUTH CAROLINA—Greenville County, 24 August. TENNESSEE—Fentress County, 11 to 19 June, 2 and 16 July and 13 August; Haywood County, 25 May; Knox County, 29 May; Morgan County, 12 June; Scott County, 30 May; Sevier County, 20 May to 12 June and 30 June. VERMONT—Chittenden County, 15 to 24 June; Essex County, 2 July; Orange County, 11 July; Rutland County, 12 July; Washington County, July. VIRGINIA—Arlington County, 11 June and 11 August; Fairfax County, 2 and 16 June and 5 September; Giles County, 18 June to 22 July, 2 and 15 to 26 August; New Kent County, 31 May; Page County, 15 July; Rockingham County, 6 July; Shenandoah National Park, 29 June and 6 July; Washington County, 2 July; Wise County, 2 July. WEST VIRGINIA—Greenbrier County, 4 July; Hardy County, 2-3 July; Pocahontas County, 23 June and 5 July; Preston County, 25 June and 5 August; Randolph County, 5 July and 6 August. WISCONSIN—Juneau County, 6 July; Trempealeau County, 7 July.

Dolichopeza (Oropeza) polita polita (Johnson)

Note: Two similar forms of *Dolichopeza*, regarded heretofore as full species, have been described as *polita* and *pratti*. Closely related to these is a third form, described below. The reasons for considering these three forms as subspecies, here, are discussed in detail in the conclusions.

Literature references.—*Oropeza obscura* var. *polita* Johnson. Johnson, 1909: 122-123, pl. 15 (wing); Alexander, 1919: 930; Johnson, 1925: 33; Alexander, 1929c: 297; Rogers, 1930: 22 (as part of *obscura* Johnson).

Oropeza polita Johnson. Alexander, 1931a: 138-139 (the variety redescribed as a full species).

Dolichopeza (Oropeza) polita (Johnson). Alexander, 1941a: 296; Alexander, 1942: 214, fig. 26E (hypopygium).

Original description.—"Distinguished from the typical form by having the entire dorsum highly polished. One specimen has the vein forming the anterior side of the discal cell wanting or indicated by a stub. Length, male, 9 mm.; female, 11 mm."

Redescription by Alexander (1931a):—"Generally similar to *O. obscura* Johns., differing especially in the short antennae and structure of the male hypopygium.

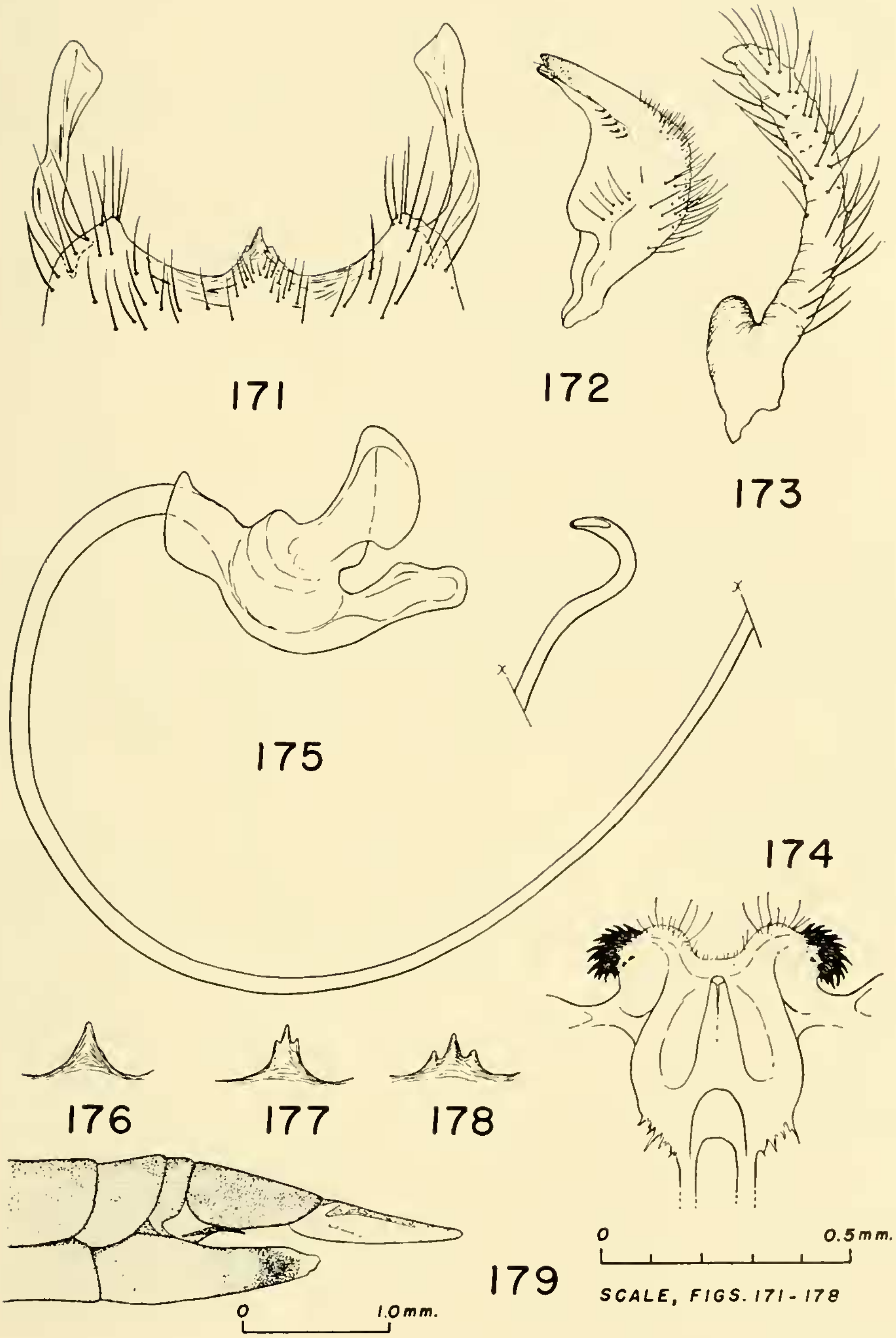
"Antennae much shorter than in *obscura*, if bent backward scarcely attaining the root of the haltere. Mesonotum dark brown, nitidous, without stripes. Knobs of halteres darkened. Tarsi more evidently darkened. Wings with the stigmal area paler, not contrasting strongly with the ground-color. Venation: cell 1st M_2 narrow at base. Abdominal tergites almost uniformly darkened, not conspicuously bicolorous as in several related species, the outer segment and hypopygium almost black; basal sternites a little brighter but not conspicuously dimidiate. Male hypopygium with the median region of the tergite produced into a quadrate plate that is further produced into a sharp median point; incurved lateral arms of tergite elongate, at tips dilated into spatulate dusky blades, the margins smooth. Outer dististyle black, sinuous, at base dilated and expanded, at tips nearly acute. Inner dististyle much more expanded than in *obscura*, the blade approximately as wide as long."

Types.—Holotype male, North Adams (Berkshire County), Massachusetts, 8 August 1907, Owen Bryant. Allotype, same data. One male and two female paratypes, together with the holotype and allotype, in the collection of the Museum of Comparative Zoology, Harvard University.

Diagnostic characteristics.—Both sexes of this race of *polita* may be identified in the field by their dark grayish brown coloration, large size and polished appearance, the last especially evident on the thoracic dorsum, which has a somewhat paler color and higher gloss than the abdomen. Males may be recognized by the structure of the hypopygium: the tergal arms are expanded at the tips and very strongly sclerotized, nearly black, and the bulbous enlargement on the mesal surface of the base of each outer dististyle is conspicuous and usually darkened (Figs. 171 and 173). Lack of distinct abdominal annulations and the low contrast in color of the stigmal spot of the wing as compared to the ground color are characters that will aid in distinguishing *polita polita* from other species but that are found also, in greater or lesser degree, in all three forms of the species *polita*. Females of this subspecies have the subapical sclerotization of the hypovalves more intense than that of the other two races.

Descriptive comments.—The highly polished appearance of this fly, while pronounced enough to identify the subspecies, is actually a relative quality. There is a glossiness, in certain lights, in the exoskeleton of *obscura*, sometimes in *tridenticulata*, and in the other races of *polita*. Rogers (1930: 22) concluded that some degree of the polished effect is related to ". . . post-mortem changes, associated with slow and imperfect drying." I have seen a few specimens of the other forms of *polita* in which some thoracic lustre seems to have resulted from the internal separation of the flight muscles from the sclerites, but the polished appearance thus produced never equals that of the typical form of *polita*, in which it is very evident in the living flies. It is stated by Rogers (1930: 22) that "among the large series (about 100) taken of *O. obscura* are a number of specimens that now have the appearance of *O. obscura polita* with the dorsum of the thorax highly polished." Actually, this series does contain, in addition to *obscura*, several specimens of the typical race of *polita*, some of *polita cornuta*, and some apparently intergrades (see distribution map for this species).

The general coloration of this subspecies is darker than that of the other two, the abdomen especially being strongly tinged with dark green, particularly in females. In the races *pratti* and *cornuta*, the abdomen is more often of the grayish brown color found in



FIGS. 171-179. *Dolichopeza (Oropeza) polita polita;* 171—ninth tergum of male, 172—left inner dististyle of male, dorsal aspect, 173—left outer dististyle, dorsal aspect, 174—gonapophyses and adminiculum, dorsal aspect, 175—vesica and penis, 176-178—variations in medio-posterior margin of ninth tergum of male, 179—terminal abdominal segments of female, left lateral aspect.

tridenticulata, so that in males there are annulations of darker color often in evidence.

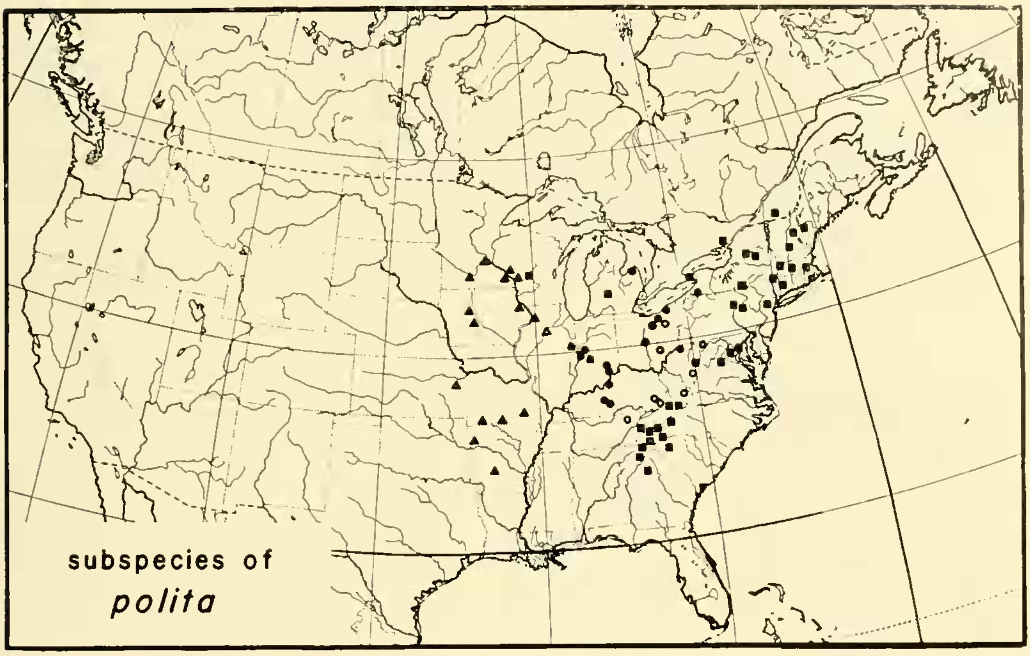
Venational variations observed in *Dolichopeza polita polita* include loss of the medial cross-vein with the discal cell remaining open and absence of this cross-vein due to closure of the distal end of the discal cell by temporary contact of the veins M_{1+2} and M_3. Absence of portions of M_2 and M_3 are not uncommon, but the abnormality figured by Johnson (1909: 122 and plate 15, as mentioned in the original description quoted above) is very unusual. Slight displacements of the m-cu cross-vein with relation to the discal cell, as well as minor fluctuations in the positions of other veins, are often seen.

Body length of males varies from 8 to 11 mm.; wing length from 10.5 to 14 mm. Females measure 8 to 12 mm.; wing length 9 to 13 mm. Throughout this species, that is, in all three races, the females are rather generally smaller than the males, although the range of body length given here does not indicate this. In all other species of North American *Dolichopeza,* the reverse is true, as it is also among Diptera in general. The size difference between spring generation individuals and those of the late summer generation is pronounced, all the larger specimens seen having been collected in June or early July.

Most variation in the male hypopygium occurs in the structure of the ninth tergum. The tergal arms vary only slightly, always within the limits of the description by Alexander, that is, with the tips widened, flattened and entire. The profile of the medioposterior margin of the ninth tergum, in contrast, varies greatly, as indicated in Figures 176 to 178. Specimens having three acute teeth in this position are not common, the form most often seen being that figured in the illustration of the typical tergum (Fig. 171). Specimens approaching either *polita pratti* or *polita cornuta* in this character are quite uncommon.

While other species of the *obscura* group have comparatively long antennae, in the males, the antennae of this and the other races of *polita* are short for the over-all body size, as emphasized by Alexander.

Geographical distribution.—Although ranging southward to Georgia along the eastern slopes of the Appalachian Mountains, this race is, I believe, the most northern of the three in the character of its distribution. The central Michigan and west-central Wisconsin localities (see distribution map) seem out of place and are in-



MAP 6. Range of *Dolichopeza (Oropeza) polita* sspp. Squares—*polita polita* (Johnson); solid circles—*polita cornuta* new subspecies; hollow circles—areas of intergradation between *p. polita* and *p. cornuta;* solid triangles—*polita pratti* Alexander; hollow triangle—area of intergradation between *p. cornuta* and *p. pratti.* Each spot represents one or more collections within a county (United States) or at a locality.

deed difficult to explain. As *polita polita* seems less bound to rocky ravine habitats in the northernmost parts of its eastern range than is either of the other two races, I believe it may extend westward from New England, across southeastern Canada, where such habitats are rare, to connect with the Michigan and Wisconsin populations. Further collecting in the northern Great Lakes area is necessary to show the true relationships of the races in the northern parts of their ranges. Where this form occurs together with *polita cornuta* (hollow circles on the map), intergrades are usually found, as already indicated for the eastern Tennessee locality. In Hocking County, Ohio (the southern of two hollow symbols shown in that state), only two specimens from a sample of 101 were of the *polita polita* type, while in the northern part of Ohio (Portage County) the two forms may occur in almost equal numbers, without intergrades. This problem is discussed in detail in the conclusions.

Habitats.—Through the greatest part of its range, *polita polita* is found in rock gorges, in the shade of undercut sandstone or limestone cliffs, and in darkened crevices between or beneath boulders in the mountainous areas. In the northeastern part of the United States, however, it occurs in much smaller crannies, such as among boulders of rather small size on wooded slopes and along mountain brooks. While this race seems to have somewhat higher moisture requirements than either of the other races of *polita*, I have taken it occasionally in shaded niches having no evident moisture and located a hundred yards or more from any source of water. Alexander (1929c: 297) described habitats of this fly in Taconic Park, Columbia County, New York, very similar to those in which I have collected it.

Seasonal distribution.—In only a few localities is there any evidence of two annual generations. In Eaton County, Michigan, I found the first emergence of adults to take place around the middle of June and the second from mid-August to early September. In the eastern states, the collection records are scattered, so that there is no evident pattern of seasonal distribution. There are records for late May to the end of August, with the greatest number of specimens having been taken in July. The earliest dates are for southern Ohio and the southern Appalachian Mountains (30 May and 5 June, respectively), but there are records for only a few days later as far north as Quebec.

Immature stages.—Eggs of *Dolichopeza polita polita* laid by females of the late summer generation, in Eaton County, Michigan, averaged .75 by .30 mm. in size, with very short, slightly curled terminal filaments. A single teneral female contains about 110 eggs that are matured or nearly so. Of eggs laid on 17 August, the first began to hatch on 24 August, and many were hatched by the next day. The first molt came about 17 days later.

Larval habitats of this subspecies include the mosses *Campylium chrysophyllum, Desmatodon obtusifolius, Gymnostomum calcareum* and *Myurella careyana* and the hepatic *Scapania nemorosa.* All these bryophytes were growing on slightly moist to damp, shaded sandstone, except the *Gymnostomum*, which was wet. Pupal skins of *polita polita* and/or *polita cornuta* were found in the mosses *Eurhynchium serrulatum* and *Hypnum* sp. growing on damp, trapped soil on a sandstone cliff in Portage County, Ohio; and in Eaton County, Michigan, larvae were found in the moss *Plagiothecium roeseanum* growing under similar conditions.

Larvae of *polita polita* closely resemble those of *tridenticulata* but are larger, often attaining 18 mm. in length. I am so far unable to distinguish the larvae of the three races of *polita*, but separation of any of these from *tridenticulata* may be accomplished by comparison of the pleural regions of the eighth abdominal segments, as stated in the key to larvae.

The pupa may be recognized by having the tracheal connection between the thoracic breathing horn and the mesothoracic spiracle convoluted, as well as by the characteristic form of the spiracular yoke (Figs. 107 and 117). Before the final darkening just prior to emergence of the adult, the pupa has a dark grayish green color, the thorax and wing sheaths light brown.

Notes on distribution.—CONNECTICUT—Litchfield County, 24 July and 19 August. GEORGIA—DeKalb County, 19 August; Lumpkin County, 5 June; Union County, 28 June. KENTUCKY—Letcher County, 3 July (includes intergrades with ssp. *cornuta*). MAINE—Oxford County, 11 July. MARYLAND—District of Columbia, 25 August; Garrett County, 26 June (also intergrades with ssp. *cornuta*). MASSACHUSETTS—Berkshire County, 8 and 11 August; Norfolk County, June; Worcester County, no date. MICHIGAN—Eaton County, 3 to 14 June and 16 to 30 August. NEW HAMPSHIRE—Coos County, 2 and 20 July; Grafton County, 5 July. NEW JERSEY—Essex County, June. NEW YORK—Broome County, 13 July; Columbia County, mid-August; Hamilton County, 12 July; Herkimer County, 3 July. NORTH CAROLINA—Burke County, 14 and 21 June and 1 July; Haywood County, 25 to 30 July; Macon County, 11 to 13 June and 23 August; Swain County, 30 June; Transylvania County, 14 June. OHIO—Hocking County, 30 May, 6-7 June and 31 August (also intergrades with ssp. *cornuta*); Portage County, 24-25 June and 14 July (ssp. *cornuta* also here). ONTARIO—Gananoque, 8 July. PENNSYLVANIA—Luzerne County, 27 June and 5 to 10 July; Wyoming County, 15 July. QUEBEC—Knowlton, 12 June, 12 and 29 July. SOUTH CAROLINA—Greenville County, 7 June. TENNESSEE—Fentress County, 22 July to 14 August (includes intergrades with ssp. *cornuta*); Sevier County, 30 June. VIRGINIA—Arlington County, 25 August; Giles County, 21 June to 13 July and 1 August (includes intergrades with ssp. *cornuta*); Grayson County, 29 June and 7 August; Shenandoah National Park, 6 July; Washington County, 2 July; Wise County, 2 July (includes intergrades with ssp. *cornuta*). WEST VIRGINIA—Pocahontas County, 5 July (includes intergrades with ssp. *cornuta*); Randolph County, 5 July. WISCONSIN—Juneau County, 6 July.

Dolichopeza (*Oropeza*) *polita pratti* Alexander
(new combination)

Literature references.—*Dolichopeza* (*Oropeza*) *pratti* Alexander. Alexander, 1941b: 192-193.

As *Oropeza obscura* Johnson. Dickinson, 1932: 212 (part).

Original description.—"Belongs to the *obscura* group; general coloration of mesonotum opaque brown, without clearly defined stripes; legs dark; wings with a brownish tinge, the oval stigma a little darker brown; vein Sc_1 preserved; abdominal segments bicolored; male hypopygium with median area of tergite narrowly produced into a tridentate lobe; lateral tergal arms appearing as narrow spatulate blades; outer dististyle a little dilated on basal portion, the apex a short, spinous point; inner dististyle deep, its rostral prolongation long; aedeagus simple, unarmed.

"Male. Length about 8-9 mm.; wing 10-10.5 mm.; antenna about 2.8 mm.

"Frontal prolongation of head brownish black; palpi dark brown. Antennae with scape brownish yellow; pedicel light yellow; flagellum black; verticils of flagellar segments coarse. Head dark gray.

"Mesonontum brown, the surface of praescutum opaque, the posterior sclerites more nitidous; in some cases the praescutum with faint indications of lighter stripes. Pleura paler brown. Halteres dusky.

"Legs with the coxae pale brown; trochanters obscure yellow; remainder of legs brown, including the tarsi.

"Wings with a brownish tinge, the oval stigma a little darker brown; prearcular field a very little brightened; veins brown. Venation: Sc_1 preserved, Sc_2 ending opposite or just beyond the origin of Rs; petiole of cell M_1 exceeding m.

"Abdominal tergites obscure brownish yellow to testaceous yellow, the lateral margins and incisures darkened, on the outer segments and hypopygium the dark color including all of the segments; basal sternites yellow, the incisures narrowly darkened, the outer segments more generally suffused. Male hypopygium with the median area of tergite produced into a narrow lobe, the apex of which is further toothed, usually tridentate, with the central point longest; lateral tergal arms with outer blades expanded into weak spatulae, in some cases these only a little wider than the arms. Outer dististyle a little dilated on basal portion, the apex a short spinous point. Inner dististyle with the blade deep, the rostrum long-produced, its apex weakly bidentate. Aedeagus simple, unarmed."

Types.—Holotype male, St. Paul (Ramsey County), Minnesota, 14 September 1940, H. D. Pratt. Five male paratypes with same data. All are in the collection of Dr. C. P. Alexander at Amherst, Massachusetts.

Diagnostic characteristics.—This subspecies may be recognized as belonging to the *polita* complex by the structure of the male hypopygium and, in the female, by the coloration, specifically the weak or absent abdominal annulations and the low contrast between stigmal spot and ground color of the wing. From the typical race, it differs in lacking the polished appearance in both sexes; furthermore the tergal arms are less densely sclerotized and the basal portion of the outer dististyles less expanded and darkened than in *polita polita.* The configuration of the tergal arms will distinguish *polita pratti* from *polita cornuta,* for while these structures are widely flared at about mid-length and narrowed at the tip in *polita cornuta* they are nearly always widest at the tip in *polita pratti.* The acute apex and expanded base of the outer dististyles will at once separate this fly from *tridenticulata,* the only species with which it might be confused on the basis of other characters of the male hypopygium; *polita pratti* is also noticeably the larger of these two in the areas where they are found together.

Descriptive comments.—Although the abdominal segments are darker at the edges, as described (and this applies to males, very rarely to females), the annulation as in the other races of *polita* is indistinct, never as in other species of the *obscura* group. The brownish color of the thoracic dorsum seems to contain a trace of red or yellow, the prescutum more nearly resembling that of *tridenticulata* than of *obscura,* which is brown. The tinge of the wings of *polita pratti* is grayish brown, fainter than the smoky brown of the wing of *obscura.*

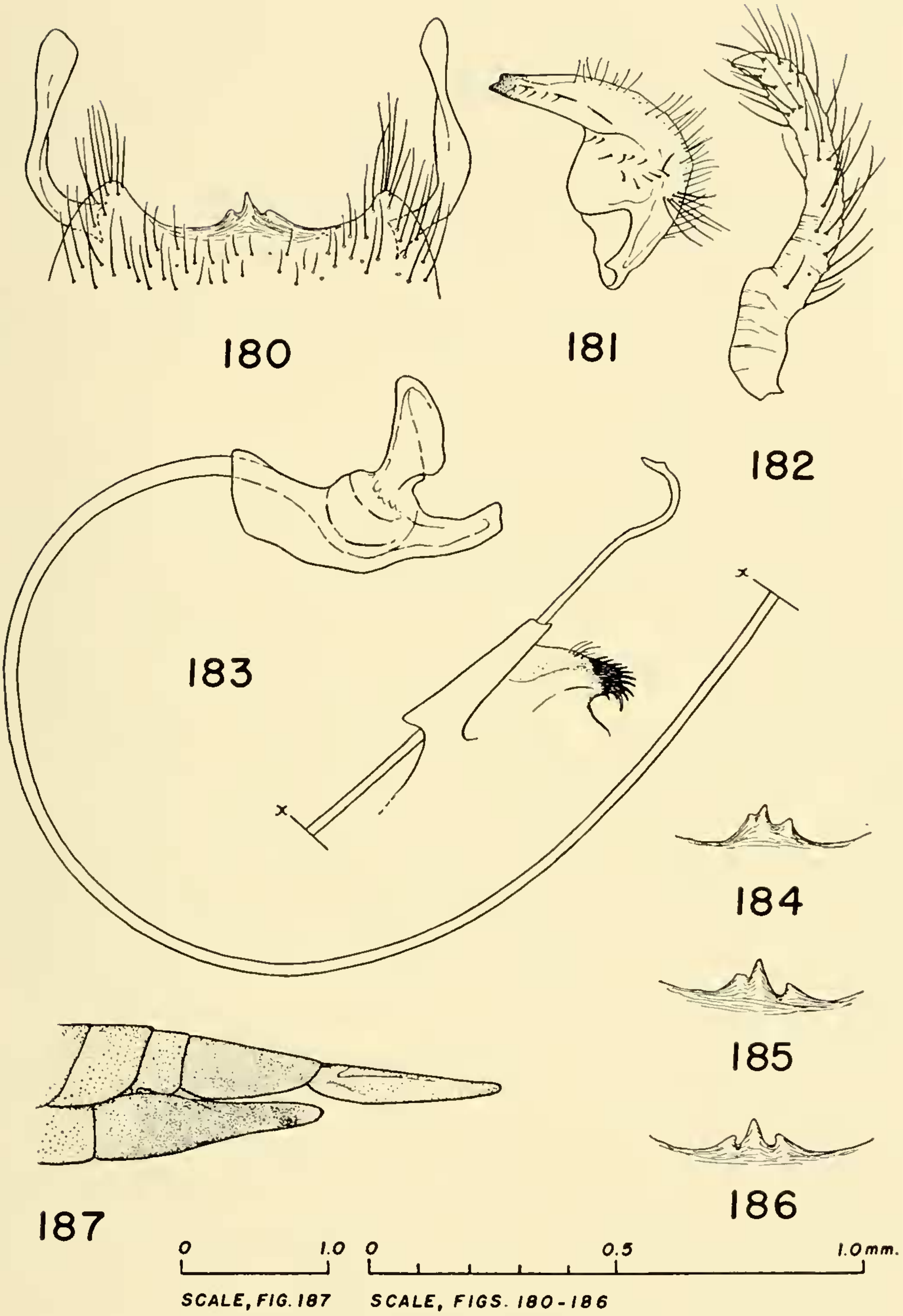
Preservation of the vein Sc_1 mentioned in the original description is an individual variation. Most specimens seen lack this vein and have wing venation characteristic of their subgenus. Other venational variations observed include loss of the medial cross-vein, the vein R_3 incomplete apically, minor displacements and interruptions of the branches of the media, and a very short cell M_1 with correspondingly lengthened petiole, M_{1+2}.

Body length of males is about 8 to 11 mm., and the wing length varies from 10 to somewhat over 13 mm. in the specimens seen.

Females are slightly smaller than males, on the average (this is the case in more than a dozen mating pairs examined), measuring 9 to 11 mm. in body length and 9.5 to 12 mm. in length of wing. The smallest measurements recorded were those of the types, which, it will be noted, were taken in September. Late August individuals collected in Kansas were smaller than the June and July specimens but larger than the types.

Variation in the shape of the medio-posterior margin of the ninth tergum of the male is extreme, exceeding even that found in the typical race. In this characteristic, *polita pratti* is much like *polita polita,* although except for the fact that the tergal arms are widest at the tip this subspecies otherwise more nearly resembles *polita cornuta* in hypopygial characters. Among the six types (all males) there are no less than four distinct shapes of the toothed medio-posterior margin of the ninth tergum. In Trempealeau County, Wisconsin, I collected a group including forty males, among which there were twelve major shapes of this structure, some extremes of which are shown in Figures 184-186. Within this same group of flies were found six kinds of tergal arms and three main classes of outer dististyles, the last on the basis of the degree of protrusion of the bulbous basal enlargement, which sometimes approaches the condition found in *polita polita* (compare with Fig. 182). Assigning letters to each different shape of these three structures, I set down a formula describing each of the forty flies. There were only six duplications in the resulting three-letter formulas; that is, there were thirty-four combinations on the basis of variation in these three characters only!

Geographical distribution.—Dolichopeza polita pratti is known from western Wisconsin, southern Minnesota, Iowa, northwestern Illinois, the Ozark-Ouachita Mountains region of Missouri and Arkansas, and eastern Kansas. Specimens regarded as intergrades with *polita cornuta* were found in a large collection including both races from Starved Rock State Park, La Salle County, Illinois. It is interesting that the transition from *polita polita* in Juneau County, Wisconsin, to *polita pratti* in nearby Monroe County should be so abrupt. The two localities represented by these collections are only 36 miles apart, and I sampled both habitats on the same day. It seems likely that northeastern Minnesota is within the range of the species *polita,* but of which subspecies I am not certain. I am confident that *polita pratti* will be found in eastern Oklahoma, and it may reach western Iowa and parts of Nebraska and South



FIGS. 180-187. *Dolichopeza (Oropeza) polita pratti;* 180—ninth tergum of male, 181—left inner dististyle of male, dorsal aspect, 182—left outer dististyle, dorsal aspect, 183—vesica, penis, gonapophysis and adminiculum, left lateral aspect, 184-186—variations in medio-posterior margin of ninth tergum of male, 187—terminal abdominal segments of female, left lateral aspect.

Dakota along the Missouri River. Surely also it occurs much more widely in the states from which it is already recorded.

Habitats.—All the known habitats are characterized by outcropping rock or large blocks of broken rock, in nearly all instances along streams, although the particular crannies in which the flies were taken were often well removed from the water. In fact, these cavities were in some cases apparently dry, but they were invariably deeply shaded so that any available moisture in the air would be conserved. Some of the flies were found beneath culverts, in cavities under earthen banks and in various other types of niches, where these occurred within the general rocky ravine or rocky hillside habitat.

Seasonal distribution.—Little is known about the seasonal occurrence of *Dolichopeza* in the western parts of the range of the genus, for too few collections have been made. In two successive years I obtained fair numbers of *polita pratti* in the upper Mississippi valley region in early July, and it was found numerous in central Iowa during the latter part of June by Dr. Jean Laffoon. Therefore, the capture of the type series in the same general area in September strongly suggests the usual two generations per year cycle. Dr. Rogers obtained a few specimens of this form in Taney County, Missouri, in mid-June, and I found them in the Ozark-Ouachita region in small numbers at the end of July and in Kansas late in August. The collection of both sexes in fair numbers in Kansas on 30 August indicated a period of emergence well underway. Accordingly, there would appear to be two annual generations of *polita pratti* in the southern part of its range, as well.

Immature stages.—Eggs taken from preserved females show the very short terminal filament characteristic of the species *polita*, the filament only slightly curved in this race. Larvae of this form have not been seen but probably closely resemble those of the other subspecies. Pupal skins were found projecting from a thin mat of the moss *Tetraphis pellucida* and a powdery lichen on the underside of a sandstone outcrop. Protected from rainfall and from seepage, this larval-pupal habitat was rather dry at the time of collection of the pupal skins. Of 17 skins recovered, four females had the middle spinous processes of the eighth abdominal sternum slightly separated at the base, that is, not divergent from a common base, and one male lacked one of these projections. Only one specimen had any spinous processes on the fourth abdominal sternum, and this was on one side only. Among 11 female skins and 6 of males, there was uniformity of shape of the spiracular yoke, as Figure 117.

Notes on distribution.—ARKANSAS—Garland County, 31 July; Washington County, 30 July. ILLINOIS—Carroll County, 7 July; La Salle County, 7 July. IOWA—Boone County, 21 to 25 June; Jackson County, 8 July; Webster County, 30 June. KANSAS—Douglas County, 30 August. MINNESOTA—Blue Earth County, 8 July; Ramsey County, 14 September; Winona County, 7 July. MISSOURI—Barry County, 29 July; Carter County, 6 June; Taney County, 10 to 20 June. WISCONSIN—Monroe County, 6 July; Trempealeau County, 7 July.

Dolichopeza (*Oropeza*) *polita cornuta*, new subspecies

Literature references.—As *Dolichopeza* (*Oropeza*) *polita* (Johnson). Foote, 1956: 221.

The name *cornuta* is selected to describe the lateral arms of the ninth tergum, which, being widened near the base and narrowed at the tip, suggest horns.

Description.—*Dolichopeza* (*Oropeza*) *polita cornuta* is olive-brown in general coloration and, depending upon preservation, may appear light to rather dark olive-brown, although not as dark as *polita polita.* Thoracic dorsum, especially the prescutum, more reddish brown, opaque and usually dull. Abdomen faintly annulated with fuscous. Occiput of head, the maxillary palps, and flagellar portion of the antennae gray-brown to dark gray. Scape yellowish brown and pedicel straw yellow. Legs brown. Wings tinged with pale grayish brown, the stigmal spot only slightly darker than the ground color. Lateral arms of ninth tergum of male flattened and expanded at about their mid-length but narrowed apically to blunt, horn-like tips. From the median lobe of the ninth tergum, three slender, acute teeth, the center tooth slightly the longest, project caudad, nearly parallel. Bases of the outer dististyles are expanded, forming a bulbous enlargement on the mesal surface of each, the enlargement abruptly paler than the rest of the dististyle. Tenth tergum and most of hypovalve of female ovipositor about equally heavily sclerotized, the cerci and tips of the hypovalves paler by comparison. Body length of holotype male 10.5 mm.; wing 12.5 mm. Allotype length 12 mm.; wing 13.5 mm. Flies of the late summer emergence may be smaller, as indicated below.

Types.—Holotype male, Turkey Run State Park, Parke County (Field Catalogue Number 6), Indiana, 20 June 1950, G. W. Byers.

Allotype, same data as holotype. Paratypes, forty males and ten females from the type locality, collected during the spring period of emergence. The holotype, allotype and most of the paratypes are in the University of Michigan Museum of Zoology, Ann Arbor, Michigan. Two paratypes have been sent to the United States National Museum, Washington, D. C. Because I have hundreds of specimens from several localities and in varying states of preservation, it seems reasonable to limit the paratypic series in some way; hence the selection of fifty topotypes in good condition and from the same seasonal generation as the holotype.

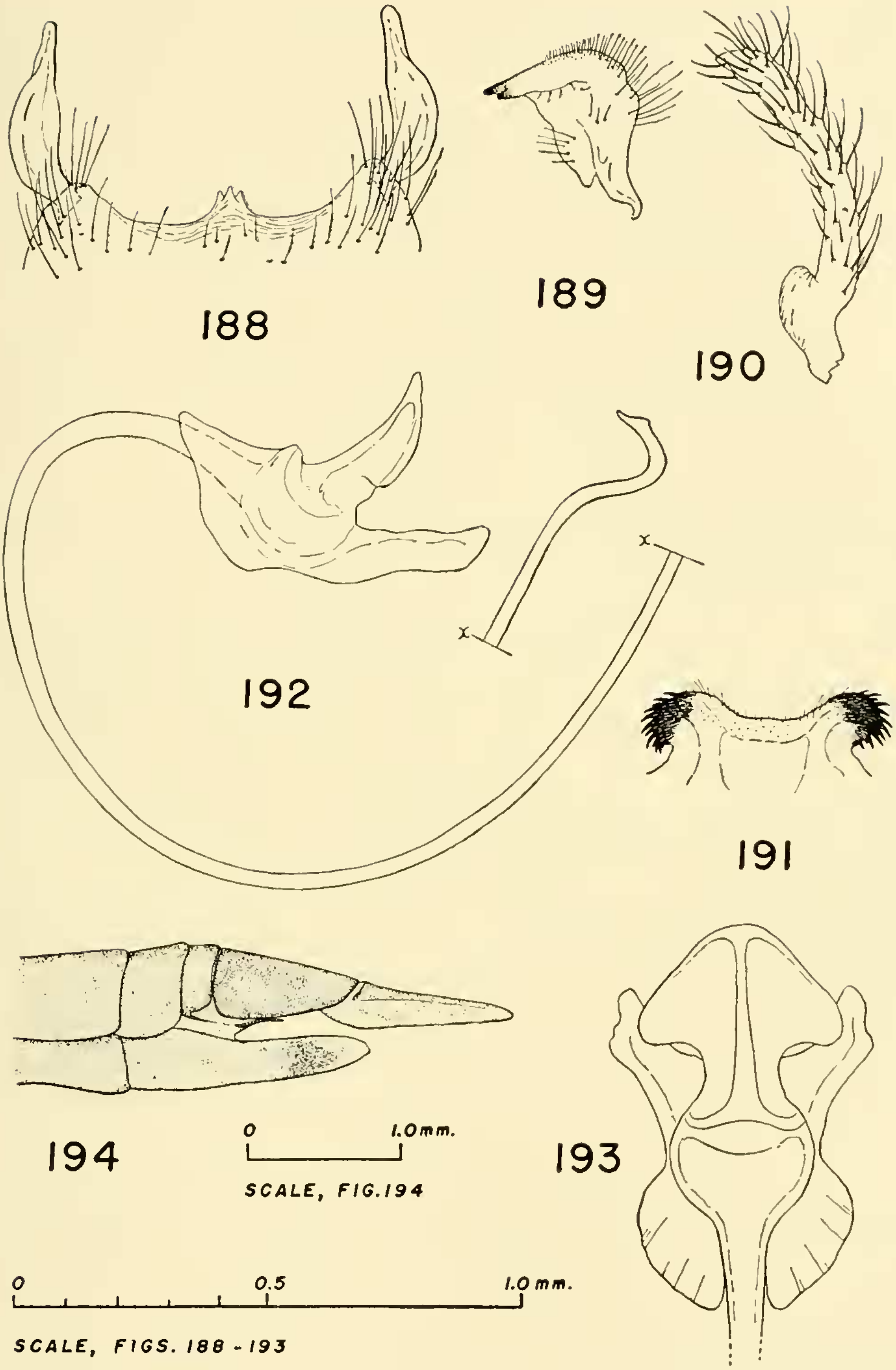
Descriptive comments.—Venational abnormalities are common in this race, although most of these are limited to the medial field. Loss of the medial cross-vein is not unusual, and I have seen many different patterns of fragmentation of the branches of the media. Rarely, wings having a well-developed Sc_1 or R_{1+2} have been found. In one male, the m-cu cross-vein has shifted so as to intersect the media at its first division.

As in the other subspecies of *polita*, females of *polita cornuta* are usually slightly smaller than males of the same generation in the same vicinity. Including both spring and late summer generations, measurements of males range from 9 to 11 mm., wing 11.2 to 13.8 mm.; females, from 9 to 12 mm., wing 9.5 to 13.5 mm.

In male hypopygial characteristics, *polita cornuta* is the most uniform of the three races. There is some variation in the length of the teeth on the ninth tergum, and the central tooth may be more or less depressed below the plane of the other two. The expanded portion of the outer dististyle is somewhat less developed than in the typical race but usually exceeds that of *polita pratti.* It is never darkly colored, as in *polita polita.* Often the mesal surface of the outer dististyle just beyond the bulbous basal enlargement lacks hairs, a condition that has also been seen in the other subspecies. The shape of the tergal arms, which most readily identifies this subspecies, is extremely constant, although the width of the flared portion may vary slightly.

The antennae are short, as in the other two races.

Geographical distribution.—Dolichopeza polita cornuta ranges from the upper "thumb" region of the Lower Peninsula of Michigan and from western New York state southwestward to eastern Illinois, southern Kentucky, and the Appalachian foothills of eastern Tennessee and western slopes of the Appalachians in Virginia and West Virginia. This area is rather well surrounded by the



FIGS. 188-194. *Dolichopeza (Oropeza) polita cornuta* new subspecies; 188—ninth tergum of male, 189—left inner dististyle of male, dorsal aspect, 190—left outer dististyle, dorsal aspect, 191—gonapophyses, dorsal aspect, 192—vesica and penis, 193—vesica and its apodemes, dorsal aspect, 194—terminal abdominal segments of female, left lateral aspect.

ranges of *polita polita* and *polita pratti* and by absence of apparently suitable habitats to the soutwest. I therefore believe that the range as indicated on the map is very close to the actual range in nature. The relationship of *polita cornuta* to the eastern subspecies is confusing at several localities, and it will be interesting to see how the ranges of the two will meet or overlap in such places as western Pennsylvania, where further collecting must be done. I have seen a specimen from Luzerne County, Pennsylvania, that is in many ways like *polita cornuta,* but because there are also certain dissimilarities and because the specimen is only one from a very large sample I have regarded it as an atypical individual and have not indicated it on the map.

Habitats.—Localities from which *polita cornuta* is known are characterized by rock outcrops or rock-walled ravines, providing deep shade for the adults and retaining moisture sufficient to grow mats or clumps of mosses for the immature stages. Adults are sometimes found in great numbers in darkened recesses beneath projecting ledges of rock. Where the space between outcropping rock and the ground below is great—say, more than ten feet, this and other species of *Dolichopeza* occurring with it are not likely to be found. But when the sheltering rock is close above the ground, providing deeper shade and protecting the flies from desiccation, they are likely to congregate. In places where I have most often collected this fly, it only rarely ventures up out of the cool ravines, although it sometimes may be found in parts of the ravines where no mosses could be seen.

Seasonal distribution.—There is abundant evidence of a two-generation annual cycle. In Indiana, where most intensive studies of this subspecies were carried on, the start of the spring period of emergence of adults closely follows that of *americana,* the peak being reached about the end of May. In 1953, for example, a particular cranny was visited every day so that comparative abundance of the various species could be estimated, although occurrence was noted throughout the area. First individuals of *polita cornuta* appeared on 23 May, when ten flies were counted. This was about a week after the onset of emergence of *americana.* Thereafter. population build-up was rapid, and by 28 May I estimated numbers in excess of 150 flies of this form. On 30 May, peak numbers were present—probably well over 200 individuals of *polita cornuta* in the one small cranny mentioned. A single sweep of the collecting net yielded 61 males and 52 females, as well as 29 flies of other species of *Dolichopeza,* on 1 June; by 9 June only 15 *polita cornuta* could be found at this site, and a few individuals of the spring generation were still present on 11 July. The late summer peak, in Indiana, falls in the first two weeks of August, *polita cornuta* again appearing shortly after *americana* and before any other species of *Oropeza.* On 3 August, great numbers of these flies were collected in Jefferson and Jennings counties, in southern Indiana; earlier collecting in that vicinity clearly showed these to belong to a second annual generation.

Immature stages.—Eggs of *polita cornuta* are about the same size as those of *polita polita,* being .75 by .30 mm., on the average, depending on the size of the female fly. There is a very short terminal filament, which projects slightly and then undergoes about one complete, circular coil; the filament is thus a little longer and more coiled than that in either of the other subspecies. Eggs from females of the spring generation were placed in a rearing dish on 24 June, and second generation adults appeared on 17 August.

The larvae are ordinarily green in color by reason of the lack of any dense coating of microscopic hairs to obscure the pigment in the body contents. Most of the minute hairs on the body are extremely short and occur singly, a characteristic found elsewhere only in *tridenticulata* and the other races of *polita.* On the eighth abdominal segment of the larva, the dorsal microscopic hairs are abruptly longer than any others on the body, which gives a somewhat darker appearance to the hind part of the larva and a sharp contrast to the paler, bright greenish spiracular disc. Fourth instar larvae may attain a length of nearly 18 mm., just before pupation.

The pupa is characterized by the convoluted tracheal connection between the thoracic respiratory horn and the mesothoracic spiracle of the developing adult within; also by the spiracular yoke, which may sometimes lack the small apical projections, leaving the lobes broadly rounded or irregularly truncate.

Habitats of the immature stages include the mosses *Atrichum macmillani, Leucobryum glaucum, Dicranella heteromalla,* and *Mnium punctatum* and the hepatic *Calypogeia trichomanis,* all growing on sandstone cliffs. The *Leucobryum* was only about half an inch deep and was more moist than it ordinairly is in its more usual hilltop environment, where it grows in thick cushions; and the *Dicranella* was less compact than usual, probably a new growth. The commonest larval habitat of *polita cornuta* is the thin coating of *Tetraphis pellucida* moss mixed with greenish white, powdery lichen that grows on the sheltered lower surface of outcropping rock ledges. Since water from above falls from the brink of the outcropping ledge and seepage resumes only at the contact with the ground or other rock below, this habitat is relatively dry, even at times of heavy rainfall. In contrast to this common habitat is the wet, marl-forming moss, *Gymnostomum calcareum*, from which *polita cornuta* and *johnsonella* were reared.

Notes on distribution.—ILLINOIS—La Salle County, 7 July (including a few intergrades with ssp. *pratti*); Pope County, 15 July; Vermilion County, 13 June. INDIANA—Jefferson County, 8-9 June and 3 August; Jennings County, 3 August; Montgomery County, 28 June; Owen County, 22 June, 3 and 28 August; Parke County, 23 May to 3 June, 9 to 28 June, 10 to 15 July, and 11 to 30 August. KENTUCKY—Barren County, 2 August; Edmonson County, June (?); Letcher County, 3 July (includes intergrades with ssp. *polita*); Trimble County, 3 August. MICHIGAN—Huron County, 22 July. NEW YORK—Cattaraugus County, 31 July. OHIO—Delaware County, 14 June; Geauga County, 17 July; Hocking County, 20 May to 7 June (includes two intergrades with ssp. *polita* among 101 specimens); Medina County, 4 July; Portage County, 24-25 June and 14 July (ssp. *polita* also here) and 16 August (ssp. *polita* not taken, this date); Summit County, 19 June. ONTARIO—Niagara Glen, 30 June. TENNESSEE—Fentress County, 22 July to 14 August (includes intergrades with ssp. *polita*). VIRGINIA—Giles County, 21 June to 13 July and 21 August (includes intergrades with ssp. *polita*); Wise County, 2 July (includes intergrades with ssp. *polita*). WEST VIRGINIA—Pocahontas County, 5 July (includes intergrades with ssp. *polita*); Wetzel County, 5 August.

Dolichopeza (*Oropeza*) *sayi* (Johnson)

Literature references.—*Tipula annulata* Say. Say, 1823: 25-26.

Dolichopeza annulata (Say). Osten Sacken, 1878: 40.

Oropeza annulata (Say). Needham, 1908: 210-211, pl. 16 (wing, mistakenly labelled "*Oropeza annularis*"); Pierre, 1926: 11.

Oropeza sayi Johnson (new name for *Tipula annulata* Say, preoccupied by *T. annulata* Linnaeus). Johnson, 1909: 118-119, pl. 15 (hypopygium and wing, possibly of *walleyi* Alexander, due to mixing of the two forms, as indicated below); Johnson, 1910: 708 (*walleyi*?); Alexander, 1919: 930; Alexander and McAtee, 1920: 393 (at least in part *walleyi*); Johnson, 1925: 32; Leonard, 1928: 698; Rogers, 1930: 23 (*walleyi*); Rogers, 1933: 35 and 49 (*walleyi*).

Dolichopeza (*Oropeza*) *sayi* (Johnson). Alexander, 1942: 214, fig. 26F (hypopygium); Rogers, 1942: 59; Rogers, 1949: 12; Foote, 1956: 221.

Original description.—"A dark brown stigma; abdomen pale, annulate with black. Inhabits Pennsylvania. Antennae fuscous, first and second joints whitish; rostrum, and lower portion of the front whitish; vertex and occiput dusky; palpi fuscous; thorax yellowish-brown, the indented lines paler; metathorax light livid; wings with a brown stigmata, nervures brown, arranged like those of Meigen's fig. 9, pl. 6; feet dusky-brownish; abdomen yellowish-white, incisures and their margins black, forming annulations complete. Length two-fifths of an inch."

Types.—No type specimen or series of syntypes has ever been specifically designated for this species, so far as I have been able to determine. If Say had any types, these are assumed to have been destroyed, as explained in the historical review. Needham did not clearly fix the identity of the species when he made *Tipula annulata* the type species of *Oropeza* in 1908. His illustration of the wing could apply to any species of *Oropeza*, and since his specimens, collected near Old Forge, New York, have been lost, it is impossible to say with assurance what species he actually had.

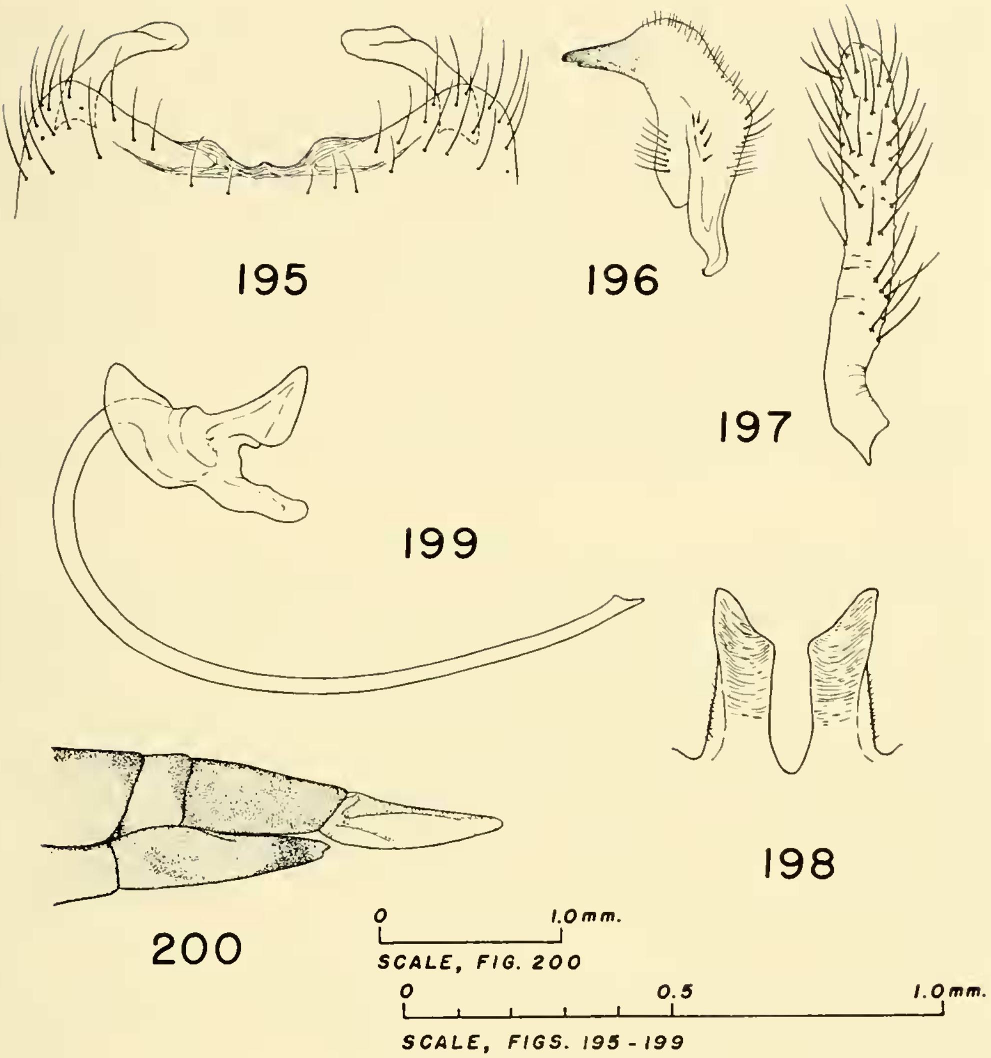
In the collection of the Museum of Comparative Zoology, beside a label reading "*O. sayi*—Johnson (*T. annulata* Say)," there are some of the twenty-five specimens that Johnson had before him when he renamed the species as *Oropeza sayi* in 1909. These are two males and two females of *Dolichopeza walleyi.* The males are those recorded (Johnson, 1909: 119) from Niagara Falls, New York, 23 June, and the females are those from Hanover, New Hampshire, 6 July 1908, and Acquia Creek, Virginia, 24 May 1896. In addition to these four, there is one male (Montpelier, Vermont, 25 June 1906) that was sent to Dr. Alexander, in trade. This specimen is the form now known as *sayi*, and it was by comparison with it that Alexander distinguished his new species, *walleyi.* The twenty specimens of Johnson's series not accounted for here were not available to me for study; possibly they are in storage in a municipal museum in Boston or in Boston University.

There is little in the original description of this species that is helpful in establishing its identity. Say's wording is so general as to be equally applicable to several species of *Tipula* or *Nephrotoma* that occur in Pennsylvania, as well as to certain species of *Dolichopeza.* His reference to ". . . Meigen's fig. 9, pl. 6" pertains to a figure in the first volume of J. W. Meigen's *Systematische Beschreibung der bekannten Europäischen zweiflügeligen Insekten* (Meigen, 1818). This figure clearly represents a species of *Nephrotoma* and had been sent to Meigen under the name *Nephrotoma imperialis*; however, he placed it in *Tipula*. As pointed out in the historical review, Wiedemann identified specimens of *Dolichopeza johnsonella* and of *Tipula* as Say's *Tipula annulata*, and Osten Sacken had in his collection certain specimens he regarded as belonging to this species. Actually, Osten Sacken's specimens are one male of *Dolichopeza tridenticulata*, one male of *walleyi*, one female of *similis* (also pin-labelled "Pachyrhine?") and four females of the *obscura* group. Of these, only the male *walleyi* and the female *similis* fit at all Say's description.

This chaos of poor descriptions and lost specimens, of mixed and misidentified species, seems to me a proper occasion for designation of a neotype. Accordingly, I have selected a male specimen from New York as neotype and a female from Pennsylvania as neallotype. (At the time of this selection, I had not seen the three males of *sayi* from Luzerne County, Pennsylvania, which are in the Dietz collection in the Academy of Natural Sciences, Philadelphia; however, the neotype chosen is in better condition than any of these.) The neotype agrees with the species *Dolichopeza sayi* as distinguished from *Dolichopeza walleyi* by Alexander (1942: 214, fig. 26F) and as illustrated in my Figures 195 through 199. The neallotype agrees with my Figure 200, and both sexes conform to the descriptive comments given below. Label data on these types are as follows:

Neotype male, Ulster County (Field Catalogue Number 1), New York, 28 June 1953, G. W. Byers. Neallotype, Berks County (Field Catalogue Number 1), Pennsylvania, 15 August 1956, G. W. Byers. Locality for the neotype is Esopus Creek, 1.3 miles west of Shandaken; the specimen is in the collection of the University of Michigan Museum of Zoology. The neallotype was taken in French Creek State Park, about 11 miles southeast of Reading; the specimen is in the Snow Entomological Museum, University of Kansas.

Diagnostic characteristics.—In the field, where *sayi* often occurs together with *dorsalis*, it may be distinguished from the latter by its dark pleural markings and the much darker stigmal spot of its wing. *Dolichopeza sayi* most closely resembles *walleyi*, but the entire margin of the gonapophyses in *sayi* (Fig. 198) will readily separate males of this species from *walleyi*, in which the edges of



Figs. 195-200. *Dolichopeza (Oropeza) sayi;* 195—ninth tergum of male, 196—left inner dististyle of male, dorsal aspect, 197—left outer dististyle, dorsal aspect, 198—gonapophyses, dorsal aspect, 199—vesica and penis, 200—terminal abdominal segments of female, left lateral aspect.

the gonapophyses are irregularly toothed. Furthermore, in the areas where these two species occur together, or where their ranges overlap, *sayi* may be recognized by the deep gray pleural spots on the mesothoracic anepisternum, ventral portion of pre-episternum and meron, for in this part of its range *walleyi* has the pleural surfaces of the thorax pale, almost as in *dorsalis.* Recognition of females is difficult, but they are separable on the basis of the color markings stated, when attention is given to their geographic locality. A further point of coloration useful is distinguishing *sayi* from *walleyi* is that the prescutal markings of the former are dark grayish brown (often approaching black in recently collected specimens), while those of *walleyi* are ordinarily a lighter reddish brown. Females of *sayi* also may be easily confused with those of *similis.* In the latter, however, the abdominal annulations are brownish, are of rather uniform breadth around the body, and are about as wide as the yellowish spaces between annulations. In *sayi*, the annulations are more grayish brown, are broadest on the dorsum and taper laterally, and are often narrow or indistinct. Wing length of females of these two species overlaps in the range of 12.0 to 13.6 mm., a measurement of less than 12.0 mm. indicating the specimen is *sayi* (when other descriptive details fit, of course), and a measurement of more than 13.6 mm. indicating *similis.*

Descriptive comments.—This species may be briefly redescribed as follows:

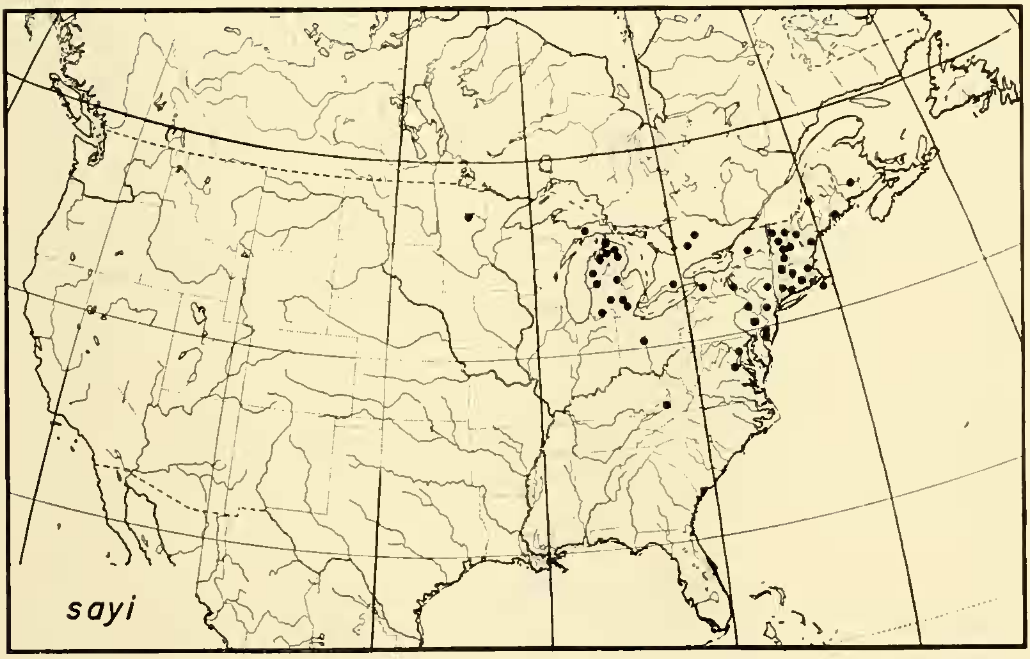
Dolichopeza sayi is in general brownish yellow, marked with dark grayish brown. Occiput gray, rostrum and frons below antennal bases yellowish; scape, pedicel and basal part of first flagellar segment yellowish, the flagellum grayish brown. Prescutum brownish yellow, marked with three longitudinal stripes of very dark grayish brown, the middle one extending farthest cephalad; scutum with two elongate, dark spots, divergent anteriorly, sometimes each divided into two; scutellum somewhat paler than prescutal ground color; mesothoracic meron and ventral part of the pre-episternum nearly as dark as prescutal stripes, anepisternum a little less darkened, the remaining thoracic pleural areas paler by contrast. Wings with a grayish tinge in living flies, the color becoming grayish amber in older specimens; stigmal spot very dark; a narrow, conspicuous band of grayish brown along the cubitus; halteres dusky. Legs dark grayish brown paling to light brown on the tarsi; coxae pale. Abdomen brownish yellow, often with the dark annulations widened dorsally, resulting in a continuous darkened stripe along the dorsal mid-line, especially in males. Annulations tapering laterally, especially on anterior segments, often incomplete and in females sometimes difficult to discern. Gonapophyses of male thick at base, flattened and slightly widened apically, the inner angle upturned, dorsal surface heavily sclerotized and a little concave, ventral surface convex, pale and sparsely pubescent (compare Figs. 7 and 198). Outer dististyles (Fig. 197) yellowish to pale yellowish brown throughout, rarely darker. Inner dististyles (Fig. 196) with an elongate, glabrous, narrowed apical portion. Ninth tergum intensely sclerotized medially, with a small central tooth flanked by two blackened lobes; tergal arms short, their distal ends only slightly expanded (Fig. 195). Female ovipositor narrowly darkened near tips of hypovalves but this area not intensely sclerotized (Fig. 200).

Body length of males varies from 8 to slightly over 10 mm. Wings of males are nearly always of greater length than the over-all body measurement, varying from about 10 to 12.5 mm. In females, on the other hand, wing length is often less even than the length of the abdomen, hence much less than over-all body length. Wing lengths of females measuring from 10 to 14 mm. ranged from 9.5 to 13 mm. Maximum expected length of wing computed from measurements of 77 females is 13.6 mm.

Venation is very constant. I have found a few instances of partial loss the the medial cross-vein, one example of a partial fusion of the subcosta with the costa, and one specimen in which the radial sector was of unusual length, suggesting that of some species of *Tipula*.

In coloration, there may be an over-all difference in intensity among specimens, so that one will appear paler in all respects than another taken at the same locality on the same date.

Apparent variation in the shape of the gonapophyses of the male may result from their partial rotation, but a few specimens have been seen in which their latero-caudal corners were rounded. The outer dististyles, though usually yellowish, occasionally have a light grayish or brownish color. A great amount of variation has been noted in the shape of the tips of the tergal arms, some suggesting those of *similis, walleyi* or *johnsonella*. As in some other species



MAP 7. Range of *Dolichopeza (Oropeza) sayi* (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

of *Dolichopeza,* it is not uncommon to find one tergal arm quite unlike the other, on one fly.

Geographical distribution.—Dolichopeza sayi is known from New Brunswick westward to northern Minnesota and southwestward to Virginia. Although it is essentially a northern species, in the character of its distribution, I would expect it to occur much more widely in Pennsylvania, Ohio and West Virginia than present records indicate. Suitable habitats for this species are also thought to occur in Canada much farther northward and westward than the now known range. Many distributional records for *sayi* published prior to 1940 will be found to apply to *walleyi.* Some of these are indicated in the literature references. In other cases, the specimens have not been seen by me.

Habitats.—Habitats in which I have collected this species are all in one way or another marshy or swampy, although in general appearance they may be quite diverse. Low, shaded vegetation of marsh borders, shrubby margins of lakes and ponds, and swampy woods are typical habitats. In the eastern part of the range, small areas of marshy terrain isolated among otherwise rocky, mesic forest lands have proved to be habitats of *sayi.* The occurrence of *sayi* in the rock gorge type of general environment, as described earlier under the natural history of adult flies, was found to be conditioned by the same microenvironmental features as those of a marsh border but present on much smaller scale. Shade sufficient to hold the temperature in the lower vegetation several degrees below that generally prevailing in the sunny parts of open marsh seems to be characteristic of *sayi* habitats. Therefore, where a pond is surrounded only by a zone of cattail (*Typha*), grasses and *Carex,* *sayi* is not likely to be found. Foote (1956: 221) reports collection of two males of *sayi* in "moist upland woods" in Delaware County, Ohio. I have not seen these specimens; the described habitat seems more appropriate for *walleyi.*

Seasonal distribution.—Where there has been enough collecting done within a limited area to give any accurate indication of the extent of the flight periods of this species, there is strong evidence of two well-marked generations per year. Rogers (1942: 59) found, in a three-year study in southern Michigan, that peaks of emergence for *sayi* came in June and August, with individuals present in May,* July and September in smaller numbers. I have

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* I have been unable to verify the 1 May date given by Dr. Rogers, either by specimens or his field notes. It is not likely that *sayi* was on the wing at such an early date. Earliest established records for this area are in the last week of May.

repeated this observation in three southern Michigan localities. Evidence from the northern portion of the range suggests that only one main period of emergence, in July, is the rule. The life cycle, indicating seasons of emergence of adults, is presented in Figure 99.

Immature stages.—Eggs of an average-sized female of *Dolichopeza sayi* from southern Michigan measured .72 by .31 mm. and showed a well-developed terminal filament. The egg stage is seven days' duration, in the laboratory. Of a large number of larvae hatched, nearly all reached the first molt within two weeks, and thereafter the molts came at about one-week intervals, until the fourth instar was reached. The last instar larva very closely resembles that of *Dolichopeza walleyi* in having the ridges of microscopic hairs most pronounced on the thoracic, first, seventh and eighth abdominal segments, while the ridges are fainter on the intervening segments. Larvae just before pupation may exceed 16 mm. in length. In the laboratory, pupation did not always take place within a tube, and the six- to seven-day pupal period was, in such cases, spent with the pupa lying on its side in the bottom of the dish. At the time of emergence of the adult, however, these pupae invariably maneuvered themselves into an upright position. This was probably to prevent contact of the adult with water, for although the immature stages of *sayi* live in a semi-aquatic environment the adults are easily trapped in water and drowned. The pupa is structurally like that of *walleyi* except for details of the spiracular yoke and the absence of projections from the posterior ring of the fourth abdominal segment.

I have found the immature stages of *sayi* in wet mosses growing flat on the muddy soil in or adjacent to swamps and marsh borders. These mosses are *Amblystegium varium, Brachythecium salebrosum, Eurhynchium pulchellum* and *Hypnum lindbergii.* Larvae were also found in *Heterophyllium haldanianum* moss on a sodden, decayed log in a swamp, and in the moss *Didymodon tophaceous,* where it was growing on a rock at the bank of a brook, just below a swampy, shaded area that drained into the brook. In all cases, the larval and pupal habitat was found to be quite wet and always well shaded.

Notes on distribution.—CONNECTICUT—Litchfield County, 12-13 June; New Haven County (?), no date; Windham County, 14 June. MAINE—Cumberland County, 1 July; Hancock County, 12 July; Piscataquis County, 17 July. MARYLAND—District of Columbia (?), 29 August. MASSACHUSETTS—Berkshire County, 19 June; Dukes County, 17 July; Hampden County, 14 July; Norfolk County, 11 June and 25 August. MICHIGAN—Antrim County, 2 July; Cheboygan County, 2-3 July; Eaton County, 30 August; Lake County, 26-27 June; Livingston County, 24 May to 9 July and 28 July to 3 September; Midland County, 10 June; Montmorency County, 16 July; Newaygo County, 21 June; Oscoda County, 14 to 26 June; Otsego County, 3 July; St. Joseph County, 30 May and 12 August; Schoolcraft County, July; Washtenaw County, 5 to 17 June and 13 to 19 August. MINNESOTA—Clearwater County, 11 July. NEW BRUNSWICK—Oromocto, 9 July. NEW HAMPSHIRE—Coos County, no date; Grafton County, 6 July. NEW JERSEY—Camden County (?), 6 June; Gloucester County, 6 June; Morris County, July. NEW YORK—Erie County (?), 27 August; Herkimer County (?), August; Tompkins County (?), 6 July; Ulster County, 28 June. OHIO—Delaware County (?), 13 June. ONTARIO—Algonquin Park, 3 July and October; Gull Lake, Muskoka District, June; Simcoe, 9 June. PENNSYLVANIA—Berks County, 15 August; Luzerne County, 28 June and 8 July. VERMONT—Caledonia County, July; Chittenden County, 24 June; Washington County, 25 June; Windham County, July; Windsor County, 7 July. VIRGINIA—Stafford County (locality uncertain), 24 May; Russell County, 15 August.

Note: County records are queried when there is reason to suspect that there may be confusion of this species with *walleyi* and specimens are not available for confirmation.

Dolichopeza (*Oropeza*) *similis* (Johnson)

Literature references.—Oropeza similis Johnson. Johnson, 1909: 119, pl. 15 (hypopygium); Alexander, 1919: 930; Johnson, 1925: 32; Pierre, 1926: 12; Dickinson, 1932: 212, fig. 113 (in error; this pertains to *walleyi*).

Dolichopeza (*Oropeza*) *similis* (Johnson). Alexander, 1936; 280; Alexander, 1942: 214-215, fig. 24B (wing), fig. 26G (hypopygium); Rogers, 1942: 60, 121.

Original description.—"Head yellow, vertex brown, palpi yellow, antennae yellow becoming fuscous toward the tips. Thorax yellowish, with three wide and poorly defined black stripes covering the dorsum; scutellum, metanotum, and plurae light yellow, with livid spots between the coxae, on the plurae, and at the end of the metanotum. Abdomen yellow, with blackish rings at the margins of the segments. Genitalia brown, appendages yellow, style black and slightly forked, appendages at base of style irregular, curved, and hamate. Ventral margin broadly emarginate. Ovipositor yellow. Halteres and legs yellow. Wings yellowish hyaline, veins and stigma dark brown. Length, male, 10 mm.; female, 13 mm."

Types.—Holotype male, Ricketts, North Mountain (Sullivan County), Pennsylvania, 8 June 1898, C. W. Johnson. Allotype, Auburndale (about 1.5 miles northwest of Newton, Middlesex County), Massachusetts, 4 June ——, C. W. Johnson. Together with the holotype and allotype in the collection of the Museum of Comparative Zoology, Harvard University, there is one female paratype. A fourth specimen mentioned by Johnson (1909: 119) is not in this collection. Although the site of the village of Ricketts, on North Mountain, is still indicated on some recent maps of Pennsylvania, the village itself has long since disappeared. Once a thriving lumbering town of several hundreds population, Ricketts vanished with the removal of all the valuable timber from the surrounding hills. Development of second-growth forest is restoring much of the area to enough of its former condition to provide many good habitats for species of *Dolichopeza.*

Diagnostic characteristics.—Although this is the largest species of North American *Dolichopeza,* it is not sufficiently larger than the similar *walleyi* or some other species occurring in the same habitats to be recognized in the field on the basis of size alone. In its natural swampland habitat, *similis* may be recognized by the combination of its large size with the golden-brown tinged wings with a dark seam along the cubitus, the yellowish body coloration and the nearly complete fusion of the prescutal stripes.

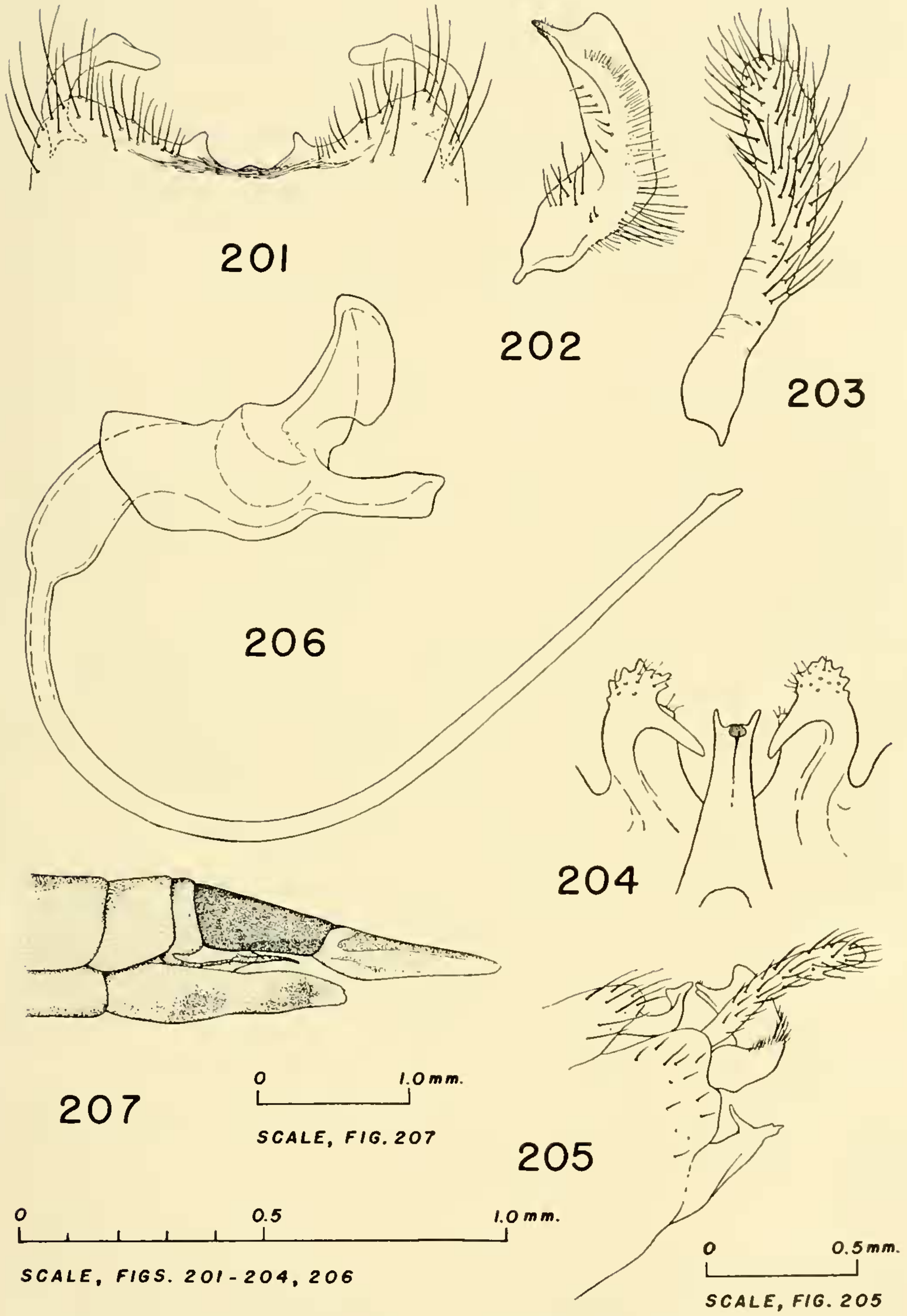
On close examination, male specimens are readily distinguishable by their unique gonapophyses (Fig. 204). In no other species is the dorsolateral angle of the gonapophysis produced into a thick, spine-like structure, projecting dorsocephalad. Also, the adminiculum is unlike that of the other species in that it bears a short spine on either side, at the apex. The female of *similis* is most likely to be confused with *sayi* and *walleyi.* Separation of these from *sayi* females is discussed in detail under that species. From *walleyi* females, these differ in having the tenth tergum more densely sclerotized than any other part of the ovipositor, the abdominal annulations of more uniform width throughout, and the prescutal stripes less distinct. Specimens of considerable age have some resemblance to females of *johnsonella* because of the indistinctness of the prescutal markings, the amber tinge of the wings and the uniformly wide abdominal annulations; however, in *similis* females the pleural markings are more distinct, and the intense sclerotization of the hypovalve below the tenth tergum found in *johnsonella* is absent, although darkened areas somewhat like those in *carolus* females are occasionally seen (Fig. 207).

Descriptive comments.—Concerning coloration, the thoracic stripes, described by Johnson (1909: 119) as black, are a dull, reddish brown to brown, in specimens of a few years' age, grayish brown in some more recent specimens. In general aspect, *similis* has a dark, tawny-yellow color, clearly annulated on the abdomen and contrastingly marked with prescutal stripes and pleural spots on the thorax. The wings are tinged with golden brown, and the stigmal spot is long oval in most specimens.

Venation in this species is generally of the subgeneric pattern, but a few abnormalities have been seen. Presence of the veins Sc_1 and R_{1+2} was noted in a few specimens, and a spurious cross-vein in cell R_3 was equally rarely seen. The cell M_1 is occasionally nearly sessile, rarely sessile. Slight variations in position or completeness of the branches of the media are not uncommon.

Sizes recorded earlier for *similis* (Alexander, 1942: 215; Johnson, 1909: 119) seem unduly small. These measurements represent *similis* as no larger than several other species of *Oropeza*, although it is in fact the largest, so far as I can compute from the few (67) specimens I have seen. Males range from about 10 to 12 mm. in over-all body length, their wings from slightly less than 12 to about 14.5 mm. Females vary in length of body from 11 to 14.5 mm., and in wing length from 12.7 to slightly less than 15 mm. Computation of expected range of wing length (a range of three standard deviations either side of the mean of the sample) indicates the wings of females may vary from 12 to 15.6 mm.

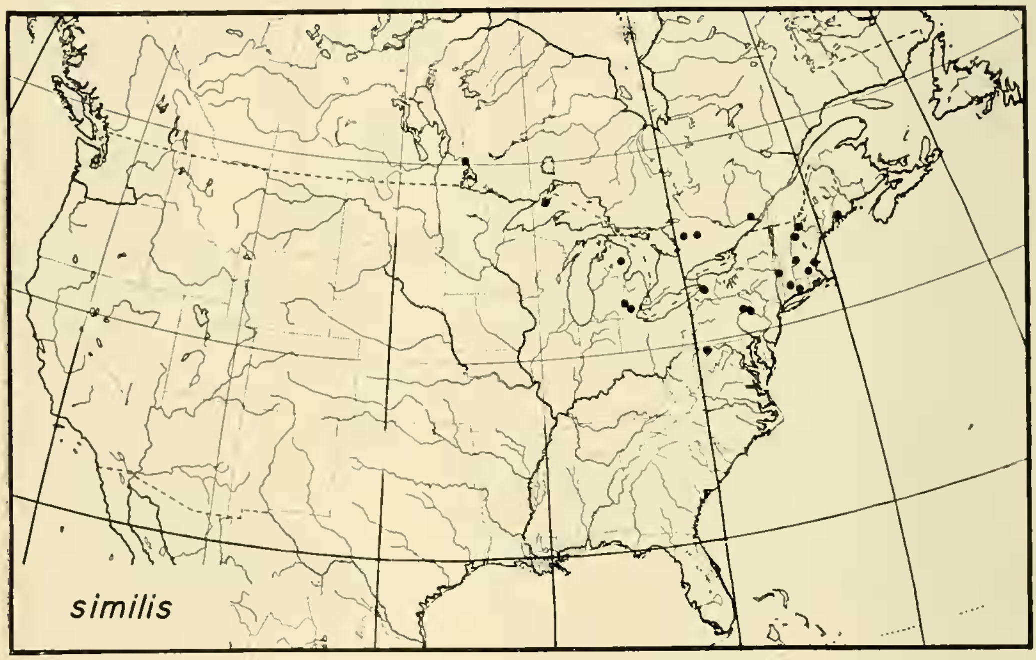
Being irregularly toothed at their margins, the gonapophyses show considerable variation, but they have been sufficiently uniform in all specimens seen to identify the species. It should be noted that these structures in males of *similis* (as also in *walleyi*, which is apparently the most closely related species) may be bent backward and downward from their normal position, in such a way that their dorsal or inner surfaces are exposed and the strong spines point caudad. While the usual profile of the ninth tergum is as shown in Figure 201, the median tooth, never very prominent, may be lacking. The inner dististyle (Fig. 202) is rather narrow throughout, with an abruptly more slender apical portion, some-



FIGS. 201-207. *Dolichopeza (Oropeza) similis;* 201—ninth tergum of male, 202—left inner dististyle of male, dorsal aspect, 203—left outer dististyle, dorsal aspect, 204—gonapophyses and adminiculum, dorsal aspect, 205—hypopygium of male, left lateral aspect, 206—vesica and penis, 207—terminal abdominal segments of female. left lateral aspect.

what suggesting the condition found in *sayi*. The basal portion of the penis is unusually enlarged (Fig. 206), more so than in *subalbipes*, the only other species in which this development has been found. This enlargement of the tube seems to be no more than a continuation of the lumen of the vesica; its particular function is unknown. One specimen has been seen in which the adminiculum bears a short, blunt spine on its ventral surface, resembling *subvenosa*, but the spine less prominent. The shape of the distal ends of the tergal arms varies a little but is usually as Figure 201.

Geographical distribution.—The range as presented by Alexander (1942:215) nineteen years ago has not been materially extended. In fact, I cannot verify his published record for northern Indiana, and Dickinson's Wisconsin record (Dickinson, 1932: 113) is actually based on *walleyi*, so the range of *similis* is diminished to this extent. On the basis of specimens I have examined, the range extends from Maine westward to the Lake of the Woods region (Kenora District) of Ontario and southwestward to Maryland. There is a reliable record for Isle Royale, Michigan, in the Michigan collection, but the record from far western Ontario is based on a single female that I found dead in a spider web. This damaged female is darker than any other I have seen but keys to



MAP 8. Range of *Dolichopeza (Oropeza)* similis (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

similis without question. It seems, from knowledge of the ecological distribution of this species, that it must range much further north in the eastern part of North America and westward across Manitoba, perhaps to northern Alberta. Although the species is northern in the character of its distribution, it probably ranges much farther south in the Appalachian Mountains than present collection records indicate.

Habitats.—I have collected *similis* only a few times, always in well-shaded situations where moisture is abundant, such as a hardwoods of red maple, yellow birch and American elm, in southern Michigan. This woods is flooded every spring, remains wet or shallowly flooded until early summer and dries by late summer or early fall. Adults of *similis* were taken among ferns and other low vegetation when the water still stood three or more inches deep in most of the woods. Rogers (1942: 60, 121) took *similis* in a very similar hardwood swamp and in a tamarack-sumac swamp. He records ". . . scores of individuals . . . on the ceilings of the dimly-lit, miniature cavelike recesses that are formed where the mossy roots or root-bound platforms project over the water or the semisuspended silt margins of the swamp pools. Such low, dank recesses were sometimes shared by *obscura, sayi,* or *subalbipes,* but *similis* was the most abundant species here and was practically confined to these spots." Alexander (1936: 280) took *similis* along Tuckerman Trail on Mount Washington, an area much different from those already described but in which similar microhabitats may be found.

Seasonal distribution.—There is no evidence of more than one generation per year. In southern Michigan, Rogers (1942: 60, 121) made a careful study of an area where *similis* occurs, finding the flight period to be 26 May to 22 June, in the years 1936 through 1941. Late summer emergence was never found to occur. Throughout the species' range, there are date records from late May to early August, but the preponderance of specimens were taken in June. In any event, it appears that locally the flight period is quite brief, which would possibly explain the dearth of specimens in collections.

Immature stages.—The eggs of *Dolichopeza similis* are the largest of any North American species of the genus, measuring on the average .92 by .35 mm. There is no terminal filament. The first instar larvae are proportionately large, and the fourth instar larva is the largest *Dolichopeza* larva I have found, in North America or abroad, reaching a length of 19 mm. Oddly enough, adults being hard to find, the larvae and pupae of *similis* were among the first immature stages of *Dolichopeza* encountered in this study. The larva resembles that of *walleyi* in having the minute microscopic hairs in short, definite, well-separated rows, and resembles *sayi* in the character of the dorsolateral lobes of the eighth abdominal segment. The transverse ridges of larger microscopic hairs are usually faintly indicated on the mid-region of the larva of *similis* but are a little more distinct in *walleyi*. The pupa may be recognized by the spiracular yoke, which is rather like that of *subalbipes*, and the bifid pleural spines (single-bristled in *subalbipes*).

The only known larval habitats of *similis* are the mosses *Heterophyllium haldanianum, Plagiothecium denticulatum* and *Tetraphis pellucida*. The *Plagiothecium* was growing on living trees, at their bases just above the water line, in a flooded hardwoods. The other mosses were growing on well decayed, wet stumps and fallen logs. All the habitats were well shaded. As they have a yellowish brown color, the large larvae are rather conspicuous in the green mosses.

Notes on distribution.—CONNECTICUT—Hartford County, 12 June; Litchfield County, 13 June. MAINE—Hancock County, 20 June. MARYLAND—Garrett County, 28 June. MASSACHUSETTS—Essex County, 12 June; Middlesex County, 4 June. MICHIGAN—Keweenaw County (Isle Royale, Lake Superior), 5 August; Livingston County, 26 May to 22 June; Oscoda County, 24 to 26 June; Washtenaw County, 5 to 22 June. NEW HAMPSHIRE—Cheshire County, 18 June; Coos County, no date; Grafton County, 2 to 8 July. NEW YORK—Erie County, 7 to 14 June and 20 August; Rensselaer County, 7 June. ONTARIO—Algonquin Park, 3 to 23 June; Burke Falls, 9 July; Kenora District (Lake of the Woods), 4 August (specimen found dead). PENNSYLVANIA—Luzerne County, 11 June; Sullivan County, 8 June. QUEBEC—Rigaud, 25 June.

Dolichopeza (*Oropeza*) *subalbipes* (Johnson)

Literature references.—*Oropeza subalbipes* Johnson. Johnson, 1909: 121-122, pl. 15 (hypopygium); Johnson, 1910: 708; Alexander, 1919: 930; Alexander and McAtee, 1920: 393; Dietz, 1921: 260; Johnson, 1925: 32; Pierre, 1926: 12; Alexander, 1928: 57; Leonard, 1928: 698; Rogers, 1930: 23; Rogers, 1933: 49.

Dolichopeza (*Oropeza*) *subalbipes* (Johnson). Alexander, 1940: 620; Alexander, 1941a: 297; Alexander, 1942: 215, fig. 26H (hypopygium); Rogers, 1942: 60, 121; Rogers, 1949: 12.

Dolichopeza subalbipes (Johnson). Judd, 1958: 624-625.

Original description.—"Similar to *O. albipes,* but readily separated by the genitalia. Tibiae more or less yellowish, tarsi entirely white. Genitalia yellow, appendages moderately long, yellow at the base, fuscous toward the tip; style yellow, appendages at the base short and tipped with small black spines, ventral margin slightly emarginate. Length, male, 9 mm.; female, 13 mm."

Types.—Holotype male, Clementon (Camden County), New Jersey, 3 June 1897, C. W. Johnson. Allotype, same locality as holotype, 8 August 1897, C. W. Johnson. Two male paratypes, those listed by Johnson from Long Branch, New Jersey, and Auburndale, Massachusetts, are together with the holotype and allotype in the collection of the Museum of Comparative Zoology, Harvard University. One male paratype (Long Branch, New Jersey) is in the Academy of Natural Sciences of Philadelphia. I have not been able to account for the other two specimens that Johnson had: the ones from Westville and Riverton, New Jersey.

Diagnostic characteristics.—Because of the appearance of the tarsi, tibiae and femora and the general coloration of the body, *subalbipes* will probably not be confused in the field with any species other than *carolus,* which is not only similarly colored but which also has the same resting posture. *Dolichopeza venosa* and *subvenosa* somewhat resemble *subalbipes* in color but lack the darkened tips on the leg segments. In differentiating *subalbipes* and *carolus* in the field, habitat is a useful but not always reliable indicator, as discussed under *carolus.*

Hypopygial structure identifies *subalbipes* males, for this is the only species of the *obscura* group in which the median region of the ninth tergum is broadly extended caudad, except *australis,* in which there is a central, pointed tooth flanked by two lower rounded lobes. The coloration of *subalbipes* is also unique in the *obscura* group. Usually, the tips of the tergal arms are bulbous and inflated (that is, hollow), a feature found in no other species of the genus. There are, however, specimens in which the tergal arms are slender, either of rather uniform thickness throughout or only slightly enlarged at the tips, often resembling those of *johnsonella* or *australis.* In *johnsonella,* the dorsal profile of the ninth tergum is undulating (Fig. 157), while in *subalbipes* (Figs. 208, 209) and *australis* (Fig. 137) there is a definitely projecting, broad extension or lobe.

Females of *subalbipes* may be distinguished from those of *carolus* by their lacking the darkly sclerotized spot, near the base of each hypovalve, characteristic of the latter species. In *subalbipes*, also, there is a greater contrast between the dark mesothoracic anepisternum and the pale dorsal portion of the pre-episternum than is found in *carolus*.

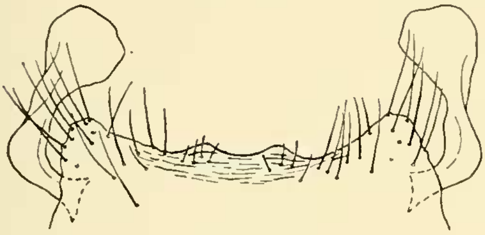
Descriptive comments.—The close similarity of color detail between *subalbipes* and *carolus* is covered in the discussion of the latter species. It might be added that both species have, in general, the same range of variation in coloration, except that there appears to me to be a tendency in northern populations of *subalbipes* to have the darker areas of the body (prescutal stripes, pleural spots, abdominal annulations, etc.) relatively darker than the corresponding areas on individuals of *carolus* from the same locality. For example, where both species were collected together in Wisconsin, *carolus* was the paler in over-all appearance.

Locally the incidence of venational variation is very high, and, as in other species of the *obscura* group especially, this variation is concentrated in the branches of the media. In a Florida population, several specimens had a short vein projecting into the cell M_2 from the medial cross-vein; and in a population from southern Georgia there was an unusual amount of fragmentation of the distal ends of the branches of the media. These and an extraordinary variation in a specimen from Alabama are illustrated in Figures 49-51.

Size variation in *Dolichopeza subalbipes* is not conspicuous through most of the range, an average male of the spring generation measuring about 9.5 mm. in body length, with an 11.5 mm. wing. Late summer males are ordinarily slightly smaller in all dimensions than those of the spring period of emergence. However, I have seen a few males from northern peninsular Florida, all collected between late October and early March, that are remarkably diminutive, the smallest having a body length of only 7 mm. and a wing length of 7.5 mm. Another very small male, like these, is from southern Georgia but was taken on the tenth of June. These males all differ structurally from most *subalbipes* of the area, as described below. Largest males seen were from Michigan and from the Appalachian Mountains in Giles County, Virginia. These flies reach a body length of slightly over 10 mm., their wings around

12 mm. Females attain greater lengths (11.2 to 15 mm.), and their wings are nearly always shorter than the over-all body length (10 to 12.5 mm.).

The most outstanding variation noted in this species is that of the hypopygium of the male, particularly of the shape of the tergal



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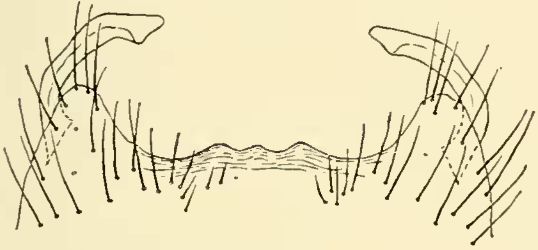

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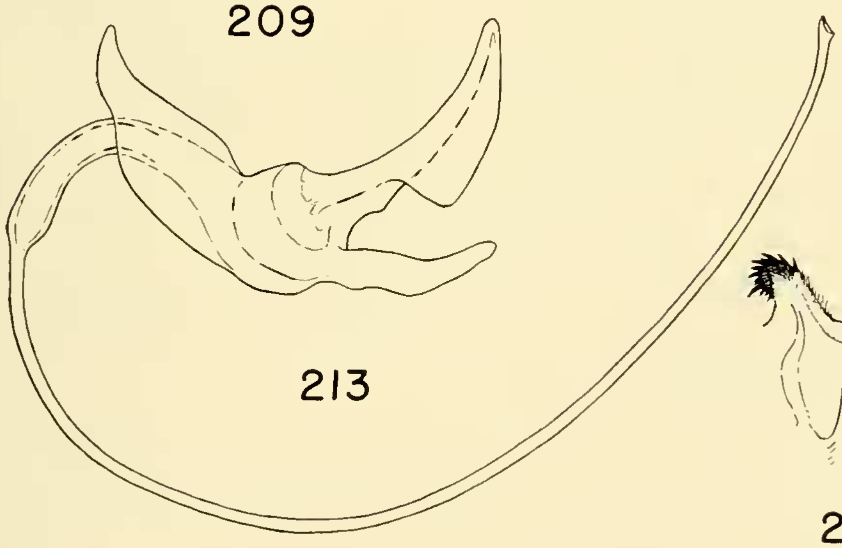

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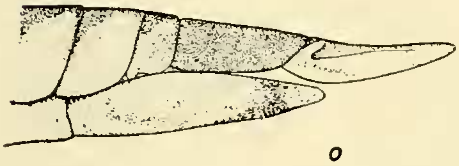

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FIGS. 208-214. *Dolichopeza (Oropeza) subalbipes;* 208—ninth tergum of male, showing expanded tergal arms, 209—ninth tergum of male with slender tergal arms, 210—left inner dististyle of male, dorsal aspect, 211—left outer dististyle, dorsal aspect, 212—gonapophyses and adminiculum, dorsal aspect, 213—vesica and penis, 214—terminal abdominal segments of female, left lateral aspect.

arm, as discussed earlier in the section on intraspecific variation. One form has tergal arms the tips of which are bulbous and knoblike (Fig. 208). The holotype of *subalbipes* belongs to this form. In Florida, the type of tergal arm with bulbous or inflated tip is by far the most common, and all specimens having the slender-tipped tergal arm are the small, winter males mentioned above. Small samples of *subalbipes* from Clearwater County, Minnesota, Juneau County, Wisconsin, and Washtenaw County, Michigan, contain males having only the type of tergal arm that is of rather uniform width or thickness throughout (Fig. 209; and Alexander, 1942: 213, fig. 26H). A sample of 15 males from Livingston County, Michigan, contained seven with the inflated tip and eight with the slender tip, with an indication that the slender tip form is somewhat more abundant in the spring generation. In Cheboygan County, Michigan (northern Lower Peninsula), Giles County, Virginia, and Fentress County, Tennessee, areas from which large samples of *subalbipes* are available, both types of tergal arm are found, the slender type commoner in the more northern localities. Very few specimens that could possibly be regarded as intergrades have been seen, an example being a fly from eastern Tennessee in which the tergal arms have inflated tips but are reduced in over-all size.

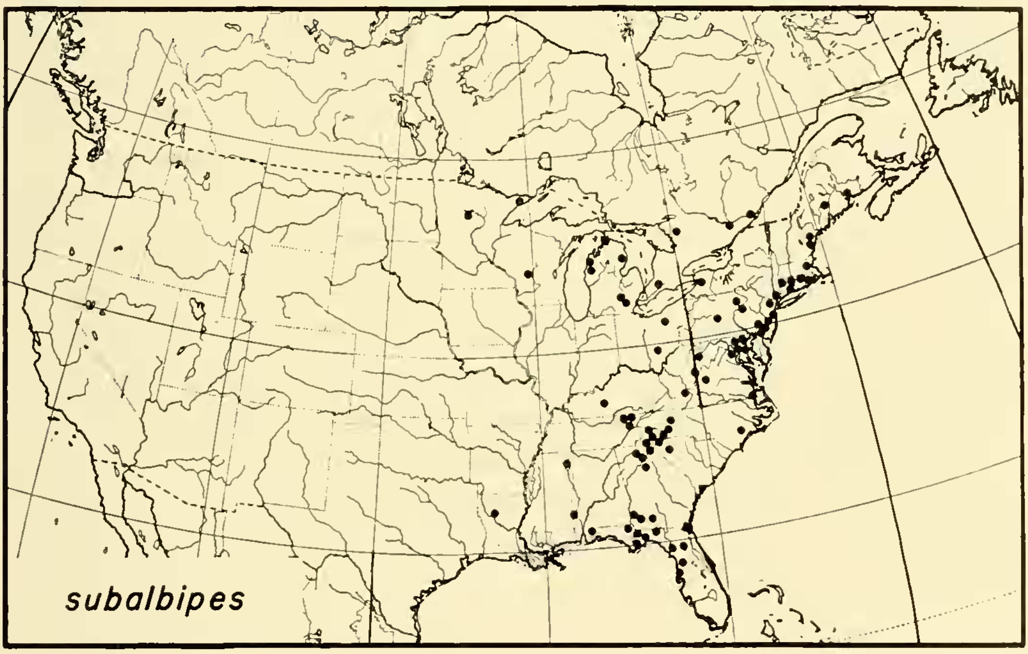
Less conspicuous but much more variable in shape is the broad, projecting median lobe of the ninth tergum. This structure may bear three obtuse peaks or, less often, two; it may project only slightly or may extend well caudad from the adjacent margin of the tergum; and it may be relatively either wide or narrow. Two commonly observed profiles of the ninth tergum are illustrated in Figures 208 and 209.

In certain specimens there is, as in *Dolichopeza similis,* a basal enlargement of the penis, although in *subalbipes* this is of a smaller diameter and somewhat greater length (Fig. 213). This character has been examined in only a few specimens that were dissected or cleared and mounted on microscope slides, but among these perhaps two dozen males there was close correlation between the presence of the basal enlargement of the penis and the inflated tip of the tergal arm. In males having tergal arms with slender tips, the penis is thick at the base but not more than twice its diameter at mid-length and without the abrupt reduction in diameter shown in Figure 213.

The descriptive data just presented lead one to question whether the nominal species *subalbipes* is not in reality two species. The two forms of males seem to exist together throughout the range, and

I have so far been unable to distinguish any two corresponding types of females. Variation in the shape of the ninth tergum of males cuts across the line drawn on the basis of the tergal arm and the basal enlargement of the penis, as does variation in the shape of the inner dististyle (which is sometimes wider near its apex than illustrated in Figure 210). In view of these things, I regard the described differences between males as polymorphic forms within one species.

Geographical distribution.—Dolichopeza subalbipes ranges farther southwest than any other species, as far as is now known, one specimen having been collected in Natchitoches County, Louisiana.



MAP 9. Range of *Dolichopeza (Oropeza) subalbipes* (Johnson). Each spot represents one or more collections within a county (United States) or at a locality.

I have not seen this fly, a female, which was reported to me as *carolus*, but I feel confident that it is not that species, and it seems unlikely that it would have been confused with any species other than *subalbipes*. Alexander (1942: 215) has also regarded this record as *subalbipes*. He reports the species from Indiana, which I am unable to verify by specimens or collection records, although I have no doubt it occurs there. The range of *Dolichopeza subalbipes* extends from New Brunswick westward to northern Minnesota and southward as far as central Florida and the Gulf Coastal Plain as far west as Louisiana. I believe there are suitable habitats in Kentucky, Indiana, Illinois, eastern Arkansas, western Tennessee and eastern Texas. Also, the natural range probably extends much farther north and northwestward than records now available indicate.

Habitats.—Adults of *Dolichopeza subalbipes* have nearly always been taken in close association with low, leafy vegetation of swampy or marshy places, or along shaded streams. It was mentioned earlier that *subalbipes* had been collected in a rocky ravine, in Wisconsin. This was an unusual locality (Rocky Arbor State Park), however, in that while rock gorge habitats could be found along its sandstone walls, the flat floor, some 200 yards in width, was covered with a typical northern swamp. Only once, in Portage County, Ohio, have I taken this species in a rocky ravine type of general habitat where even localized swampy conditions were absent altogether. In Minnesota and northern Michigan, *subalbipes* was taken in cool, well-shaded, swampy lowlands; in southern Michigan, the habitats where I found this species were swampy hardwoods and the seasonally flooded hardwood zone around a bog. I have netted *subalbipes* among dense ferns and deep grasses along forest brooks, in the Appalachian Mountains from northern Georgia to Maine, and in *Sphagnum* bogs (where other mosses also were abundant) in West Virginia and Michigan. On the Cumberland Plateau of eastern Tennessee, Rogers (1930: 23) found *subalbipes* "more confined to the upland" than *carolus* and "taken from the stream-margin thickets, sphagnum-huckleberry bogs, and from the banks of both cleared and wooded brooks. A few records are from the talus slope brooks and from the river bank of Clear Fork, but it was not collected from the 'rock houses' or the base of the wet rim rock." In Pennsylvania, Dietz (1921: 260) observed *subalbipes* to be an inhabitant of "swampy places." Northern Florida habitats of this species are described as ". . . beneath luxuriant ferns and herbage that overhang wooded rills and small brooks" (Rogers, 1933: 49). All habitats described by other authors are places in which damp mosses are likely to have been growing.

Seasonal distribution.—There is evidence of rather continuous emergence of adults, through most of the year, in the Florida region. North of Florida, however, the indication is that two annual generations occur, except in the northernmost parts of the United States and in Canada, where collection records are so few as to render the situation obscure. There are far northern records for June through August, but most of these are for July and suggest a single, midsummer generation for this region. Rogers (1942: 60, 121) found the adults of *subalbipes* on the wing in southern Michigan from 2 June to 14 July and from 14 to 28 August, the June generation the largest in numbers. He records the species as "abundant in the birch-maple swamp on June 5, and spread for 150 feet or more into the adjacent oak-hickory woods. . . . Apparently a huge 'hatch' had taken place on June 3, 4, or 5, for only a few teneral males could be found in the swamp on June 3." In eastern Tennessee, another region in which *subalbipes* has been collected extensively enough to indicate its seasonal distribution, Rogers (1930: 23) found it in May to early July and again in August.

Immature stages.—Eggs of an average sized female of *Dolichopeza subalbipes* from southern Michigan measured .83 by .36 mm., and those of a small female from Florida (one taken in February with the small males noted above) averaged only about .72 by .34 mm. In each case, the number of eggs matured appears to be around 100. There is no indication of a terminal filament. Larvae of the first two instars are not known, but the third instar very closely resembles the fourth. The fourth instar larva is one of the easiest to identify of all species of *Oropeza*. The larger microscopic hairs on the dorsum of all segments are longer than in any other species except *venosa* and are arranged in broken and irregular transverse ridges, again as in *venosa*. The minute microscopic hairs are in long, indefinite rows or sometimes not arranged in rows, while in *venosa* they are in shorter, well-defined rows.

Larval habitats are only poorly known. Rogers (1933: 49) found the larvae in "saturated mosses and liverworts, on wet earth banks, on rocks and (more rarely) sodden logs." He observed that they fed on the growing portion of the habitat plants, mainly at night. His collection of these larvae was found in include both *obscura* and *subalbipes*, however, and the bryophytes were not identified. My few collections of the larvae and pupae of *subalbipes*, made in southern Michigan, were from the mosses *Tetraphis pellucida* and *Dicranum scoparium* and the hepatic, *Geocalyx graveolens*. These bryophytes were all found on extremely decomposed and sodden wood, in a birch-maple-elm swamp, but the plants themselves were not saturated with water, as were those described by Rogers. I have never found *subalbipes* larvae in mosses as wet as those in which the immatures of *sayi* or *dorsalis* occur. Accordingly, I question the inference by Judd (1958: 624 ff.) that *subalbipes* adults emerged from water about two feet deep. It is possible that larvae were in some fragment of moss accidentally adhered to his tent trap at or above the water line, but that they might have been in submerged mosses seems unlikely to me, inasmuch as my laboratory experiments indicate the larvae of *Dolichopeza* spp. drown when wholly covered with water.

The pupa of *subalbipes* may be recognized by its slender lobed spiracular yoke and the fact that the pleural spinous processes are tipped each by a single bristle. Color comparison of the pupa of this species with that of *obscura* is made in the discussion of the pupa of the latter. The pupal stadium lasts six or seven days, under laboratory conditions.

Notes on distribution.—ALABAMA—Washington County, 14 June. CONNECTICUT—Hartford County, 14 June; Litchfield County, 31 May; New Haven County, no date; Windham County, 14-15 June. FLORIDA—Alachua County, 16 January, 17 to 28 February, 11 to 21 March, 1 to 16 April, 3 June, 25 July, 14 October, and 12 to 25 November; Escambia County, 7 April; Gadsden County, 28 to 31 March and 5 June; Hernando County, 21 March; Jackson County, 31 March to 29 April; Jefferson County, 31 March; Leon County, 18 March and 31 March to 13 June; Liberty County, 3 March to 26 April, and 15 to 27 July; Marion County, 4 April; Nassau County, 27 April; Putnam County, records for every month except December and February, with peak abundance in June (23 date records). GEORGIA—Baker County, 27 January, 9 to 24 February, 24 to 31 March, 7 and 21 April, 26 May, 27 August, and 14 October; Clay County, July; Cook County, 10 June; Hall County, 6 June; Lumpkin County, 2 to 8 June; Rabun County, 12 June; Union County, 23 May and 10 and 28 June. KENTUCKY—Edmonson County, June (?). LOUISIANA—Natchitoches County, no date. MAINE—Cumberland County, 1 July; Penobscot County, 18 June; York County, 1 July. MARYLAND—District of Columbia, 29 August; Anne Arundel County, 20 June; Baltimore County, 17 June; Prince George's County, 9 June. MASSACHUSETTS—Middlesex County, 10 to 16 June. MICHIGAN—Cheboygan County, 3 and 31 July; Iosco County, 22 July; Lake County, 27 June; Livingston County, 2 June to 8 (14?) July and 14 to 28 August; Manistee County, 21 June; Washtenaw County, 12 and 20 June. MINNESOTA—Clearwater County, 11 July; Cook County, 5 July. MISSISSIPPI—Itawamba County, 14 July. NEW BRUNSWICK—Charlotte County, 5 July. NEW JERSEY—Bergen County, 1 to 15 June; Burlington County, 11 August; Camden County, 3 June and 8 August; Gloucester County, 6 June; Monmouth County, 12 June. NEW YORK—Erie County, 9 July; Westchester County, 9 June. NORTH CAROLINA—Buncombe County, 12 June; Macon County, 11 to 13 June and 26 August to 4 September; Mitchell County, 16 June; Onslow County, 9 July; Swain County, 20 June; Transylvania County, 8-9 June; Yancey County, 7 June. OHIO—Hocking County, 6 June; Portage County, 25 June. ONTARIO—Blackburn (5 miles east of Ottawa), 6 August; Kearney (about 20 miles west of Algonquin Park), 2 July; Byron (4 miles west of London), 16 June. PENNSYLVANIA—Berks County, 15 August; Centre County, 25-26 June and 4 to 9 July; Luzerne County, 4 and 14 to 19 June; Sullivan County, 10 July. QUEBEC—Montreal, 14 July. RHODE ISLAND—Kent County, 15 to 21 June. SOUTH CAROLINA—Greenville County, 22 May to 7 June and 20 July to 11 August. TENNESSEE—Fentress County, 6 to 18 June, 5 to 9 July, and 8 to 13 August; Morgan County, 12 June; Scott County, 29-30 May; Sevier County, 15 and 30 June. VIRGINIA—Arlington County, 31 May; Augusta County, 28 June; Giles County, 31 May to 24 June; Norfolk County, 10 August. WEST VIRGINIA—Pocahontas County, 23 June and 5 July; Tucker County, 24 June. WISCONSIN—Juneau County, 6 July.

Dolichopeza (*Oropeza*) *subvenosa* Alexander

Literature references.—Dolichopeza (*Oropeza*) *subvenosa* Alexander. Alexander, 1940: 618-620, fig. 15 (wing), fig 18 (hypopygium); Alexander, 1941a: 297.

Original description.—"Allied to *venosa;* mesonotal praescutum grayish yellow with three conspicuous blackish stripes; pleura grayish yellow, variegated with brown; tips of tibiae and the tarsi paling to yellow, femoral tips narrowly brightened; wings with a strong brownish tinge; stigma darker brown, with conspicuous cream-colored post-stigmal areas; male hypopygium with the inner dististyle broad, especially opposite its outer end; aedeagus with a strong spine on ventral face near apex. Male. Length, about 9-11 mm.; wing, 11-12.5 mm.; antenna, about 3-3.5 mm. Female. Length, about 11 mm.; wing, 11 mm.

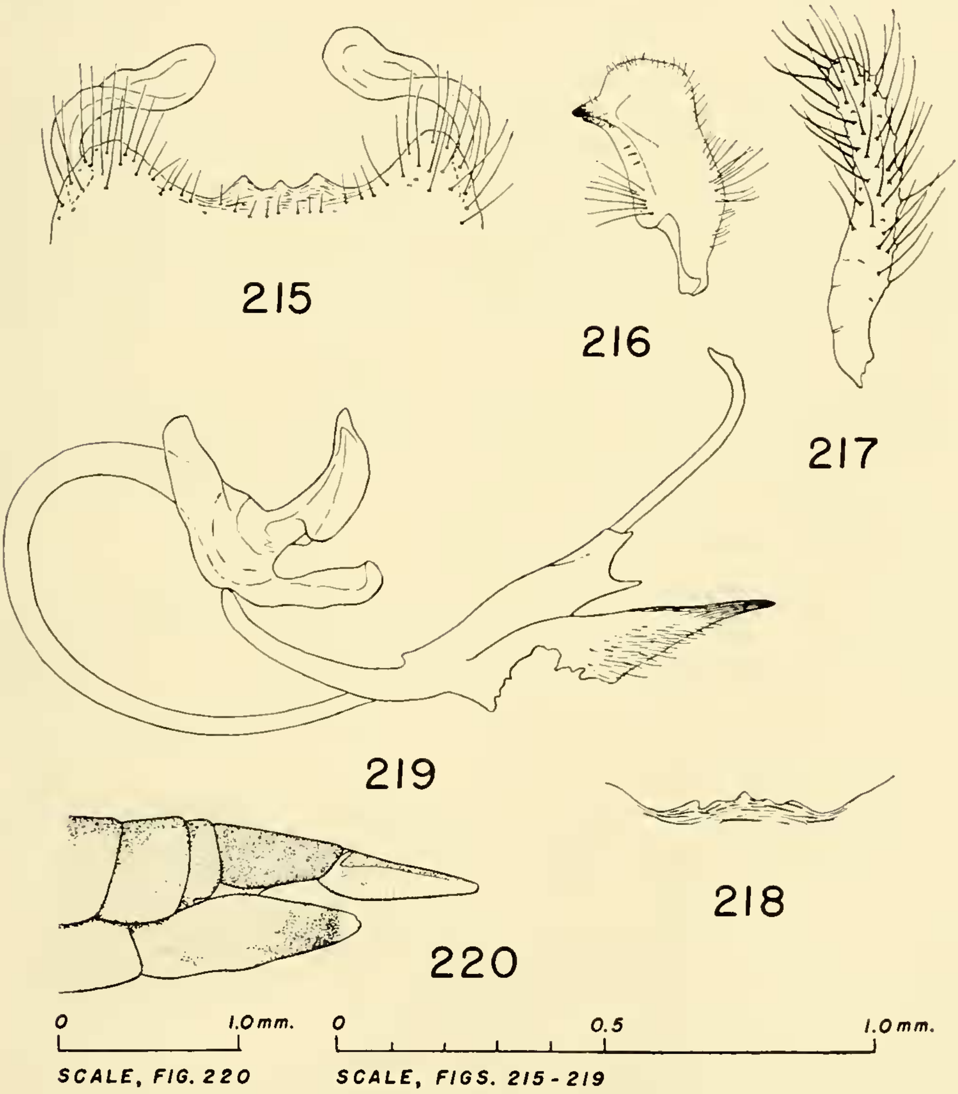
"Frontal prolongation of head pale testaceous; palpi brown. Antennae with scape and pedicel pale yellow; base of first flagellar segment pale, the remainder black; segments relatively long, subcylindrical, much exceeding the erect verticils; pubescence of segments short. Head brownish gray, darker in central portion.

"Pronotum brown, blackened medially. Mesonotal praescutum grayish yellow, with three conspicuous blackish stripes, the posterior interspaces obscured; scutal lobes brownish black, the median area very restrictedly paler; posterior sclerites not black or brownish black. Pleura grayish yellow, variegated with brown on the anepisternum, ventral sternopleurite, meron and extreme ventral edge of pleurotergite. Halteres elongate, stem yellow, knob darkened. Legs with coxae pale, the fore pair darker; trochanters yellow; femora blackened, the tips narrowly pale; tibiae dark brown, paling to obscure yellow on distal portion; tarsi obscure yellow. Wings with a strong brownish tinge; stigma oval, dark brown; a conspicuous, paler brown seam along vein Cu; membrane adjoining the stigma, especially in cells beyond the stigma, cream-yellow; a restricted brightening across the fork of M; veins brown. Venation: Sc_2 ending opposite or just beyond origin of Rs.

"Abdominal segments blackened medially and on basal rings of segments, leaving extensive yellow areas on sides of posterior rings; outer sternites and tergites, including hypopygium, more uniformly blackened. Male hypopygium with the lateral arms of tergite blackened, the apices dilated into oval spatulate blades, the margins smooth or without conspicuous angulations; median area of tergite trilobed, the central lobe longer and more spinous. Outer dististyle uniformly blackened, cylindrical, a little exceeding the inner style. Inner dististyle much deeper than in *venosa*, elevated just above the short apical beak. Gonapophyses much as in *venosa*, appearing as blackened spines, their bases with conspicuous setae. Aedeagus close to apex on ventral face with a strong, erect spine, this variable in length but always strongly developed. In *venosa*, the lateral arms of tergite are more angular, the median area of the caudal margin with the central lobe low or lacking; inner dististyle narrower, especially above and before the apical beak; aedeagus without spine."

Types.—Holotype male, Anakeesta Ridge, 4500 ft. (Great Smoky Mountains National Park), Tennessee, 12 June 1939, C. P. Alexander. Allotype, same locality as holotype, 4000 ft., 5 June 1939, C. P. Alexander. Eight male paratypes, of which six are from the Great Smoky Mountains National Park, all above 2500 feet elevation, various dates in June and various collectors; the other two from nearby Mt. Mitchell, Yancey County, North Carolina, above 4000 feet, June, collected by C. P. Alexander. Holotype, allotype and five paratypes are in the collection of Dr. Alexander, at Amherst, Massachusetts. One paratype is in the collection of the University of Michigan Museum of Zoology, and one is in the United States National Museum.

Diagnostic characteristics.—Dolichopeza subvenosa is differentiated from *carolus* and *subalbipes* by its over-all darker color, by having yellowish instead of white tarsi, and by lacking the contrastingly darkened tips on the femora and tibiae. It very closely resembles the more northern *Dolichopeza venosa,* and I have not yet discovered any reliable means of distinguishing the females of the two forms. The most readily visible characters for recognition of males of *subvenosa* from those of *venosa* are the presence of a conspicuous spine on the ventral or posterior surface of the adminiculum (aedeagus, in Alexander's terminology) and the more



Figs. 215-220. *Dolichopeza (Oropeza) subvenosa;* 215—ninth tergum of male, 216—left inner dististyle of male, dorsal aspect, 217—left outer dististyle, dorsal aspect, 218—medio-posterior margin of ninth tergum of male holotype, 219—vesica, penis, adminiculum, adminicular rod and gonapophysis, left lateral aspect, 220—terminal abdominal segments of female, left lateral aspect.

rounded tips of the lateral arms of the ninth tergum (Figs. 219, 215). Although the greater subapical width of the inner dististyle in *subvenosa* is a good indication of the species (as compared to *venosa*), it is not easy to observe except in alcoholic material or specimens mounted on microscopic slides, as the tips of these structures are usually more or less drawn down into the genital chamber.

Descriptive comments.—A tawny-yellow fly with dark brown markings, *subvenosa* is slightly paler in average, over-all coloration than *venosa*, partly by reason of the narrower abdominal annulations and partly because of the less intense color of these and the other markings. A few specimens from Giles County, Virginia, have darker tarsi than usual, these being light brown to the tips.

Wing venation in the relatively small number of specimens examined (138) was found to adhere closely to the subgeneric pattern. Slight variations in the medial field, such as the intersection of the m-cu cross-vein with the short M_{3+4} or with M_4 beyond its junction with M_3 are not uncommon. One male was seen in which the discal cell was closed distally by a temporary fusion of M_3 and M_{1+2}, in the absence of the medial cross-vein.

Body size of males ranges from 9 to nearly 11.5 mm., with the wings varying from 10.5 to 13 mm. Females are slightly larger, their over-all body length being from 11 to 12.5 mm. and their wings from 11 to 13 mm.

There is so much variation in the male hypopygial structures used in differentiating *subvenosa* and *venosa* that for a time I regarded these two forms as only subspecifically distinct. The spine on the adminiculum, for example, which is the most outstanding feature of *subvenosa*, is normally long, acute and conspicuous, as in Figure 219; however, there are occasional specimens in which it is reduced to a low, obtuse bump, even less conspicuous than the spinous development found on the adminiculum in many specimens of *venosa*. The more rounded edges of the flattened, apical portion of the tergal arm are an ordinarily reliable means of recognition of *subvenosa*, but this character also varies across the boundary between species. Males with angularly spatulate tergal arms but otherwise typically *subvenosa* have been seen from Virginia and North Carolina, while the rounded form has been observed in *venosa* males from New York and Michigan. A more detailed analysis of variation in hypopygial structures will be found in the discussion of *Dolichopeza venosa*. The intensely sclerotized, sharply pointed gonapophyses and darkly colored outer dististyles appear to me to be the same in both species. The pronounced hump in the outer curvature of the inner dististyle just before the short apical prolongation (Fig. 216) is a character of *subvenosa* that is only very rarely seen in *venosa,* the inner dististyle in the latter species ordinarily being much more slender near the tip (Fig. 231).

Geographical distribution.—For eighteen years following its description, *subvenosa* was known only from the central Appalachian Mountains of Tennessee, North Carolina, and nearby Georgia and South Carolina. Dr. Rogers collected many specimens also in southwestern Virginia, but the range of the species remained widely separated from the known range of *venosa,* to the north. Records of *venosa* in South Carolina (Alexander, 1942: 215) pertain to this form. Intensive collecting in West Virginia, southern Ohio and Pennsylvania and western Virginia in 1958 did much to clarify the respective ranges of *subvenosa* and *venosa,* the gap between the two finally being closed in Preston County, northern West Virginia, and subsequently in Garrett County, western Maryland, with the discovery of the presence of both forms, there. These ranges, so far wholly allopatric, are conveniently mapped together, the distribution map included with the discussion of *venosa.* As mentioned earlier, I had considered *subvenosa* and *venosa* subspecies of one species, at one time; however, because there is no clear zone of intergradation between the two and because their identifying characteristics are sufficient to distinguish the average specimen (on the basis of males), I have abandoned that opinion and recognize two species.

Habitats.—Most collection records for *subvenosa* are for high elevations in the Appalachians, such as the 2500 to 4500 foot elevations of the type series. I have taken the species at elevations near 1000 feet, which is approximately that of the Greenville, South Carolina, locality, and at various elevations up to around 6600 feet, near the summit of Mt. Mitchell, Yancey County, North Carolina. The species thus has a considerable vertical distribution, yet not as great as either *obscura* or *americana,* species I took together with it atop Mt. Mitchell. Within its mountainous and forested range, *subvenosa* has diurnal resting places similar to those of *venosa*: shaded, rocky crevices, undercut earthen banks, and other situations where deep shade obtains. Occasionally I found *subvenosa* suspended from ferns or other leafy vegetation near such darkened crannies. Along mountain brooks, they are often found very near the water, such as beneath an overhanging, rootbound and mossy bank, where the clearance above the water may be only a few inches. Unpublished field notes by Dr. Rogers indicate similar habitats in the places where he collected, near Mountain Lake, Virginia, and at various localities in North Carolina.

Seasonal distribution.—All but a few of the records for this species are in June, suggesting that there is but one generation per year, and the numbers of individuals taken on the various dates indicate the peak of emergence in the southern and central Appalachian Mountains comes about the end of the first week of June, perhaps a week later than that in West Virginia. At no time or place, however, have I obtained *subvenosa* in large numbers—never in aggregations and never more numerous than any other species of *Dolichopeza* occurring together with it.

Immature stages.—No study has been made of the immature stages of this species. Eggs dissected from the abdomen of a female of average size were found to have nearly the same measurements as those of *venosa*. The average dimensions were .79 by .34 mm., but eggs from a slightly smaller female measured only .75 by .31 mm. There is no terminal filament. No larvae have been found, but I would expect them to resemble rather closely those of *venosa*. Pupal skins apparently of this species were collected from a sparse growth of *Mnium* sp. on a steep soil bank above a mountain brook in western North Carolina. In these, the spiracular yoke resembles that of *venosa* except that the outer secondary lobes are more developed; also, the reticulation of the mesonotum is faint, consisting mostly of transverse wrinkles similar to those along the mid-line. There are spinous processes on the fourth abdominal sternum about half as long as those on the fifth. Four female pupae from North Carolina and Georgia ranged in size from 10.2 to 12.0 mm.; males assignable to this species were not found.

Notes on distribution.—GEORGIA—Rabun County, 5 June; Towns County, 12 June; Union County, 10 June. MARYLAND—Garrett County, 28 June (*venosa* also here). NORTH CAROLINA—Burke County, 14 June; Haywood County, 28 May; Macon County, 8 to 15 June; Swain County, 11 to 17 and 30 June; Transylvania County, 9 June; Yancey County, 7 to 22 June. SOUTH CAROLINA—Greenville County, 3 to 29 June. TENNESSEE—Sevier County, 12 to 19 and 30 June. VIRGINIA—Giles County, 8 June to 9 July. WEST VIRGINIA—

Pendleton County, 27 June; Preston County, 25 June (*venosa* also here); Tucker County, 24-25 June.

Dolichopeza (*Oropeza*) *tridenticulata* Alexander

Literature references.—Dolichopeza (*Oropeza*) *tridenticulata* Alexander. Alexander, 1931c: 177-178; Alexander, 1940: 620; Alexander, 1941a: 297; Alexander, 1942: 215, fig. 26I (hypopygium); Foote, 1956: 222.

As *Oropeza obscura* Johnson. Johnson, 1909: 122 (part), pl. 15 (wing); Rogers, 1930: 22-23 (part); Dickinson, 1932: 212 (part), fig. 114 (wing).

Dolichopeza (*Oropeza*) *tridentata* Alexander. Crampton, 1942: 147, fig. 6A (misspelling).

Original description.—"Male. Length about 10 mm.; wing 11 mm. Described from alcoholic specimens. Closely related to *obscura*, differing especially in the structure of the male hypopygium. Antennae dark brown. Mesonotum dark reddish brown, the pleura still darker. Legs with the tarsi a little paler than the tibiae. Wings suffused with brown, the oval stigma slightly darker brown; paler areas before and beyond the stigma and across the base of cell 1st M_2. Abdominal segments brownish yellow, conspicuously ringed with dark brown on the incisures, on the sternites the bases of the segments more broadly darkened than the apices. Male hypopygium with the central portion of the tergal margin produced into a small rectangular area that bears three small chitinized points; lateral arms of tergite evenly rounded at tips. Inner dististyle very broad, weakly bidentate at tip, one of the points being a small blackened spine. Outer dististyle and gonapophyses much as in *obscura*."

Types.—Holotype male, Goshen, Hampshire County, Massachusetts, 1 July 1931, G. C. Crampton. The holotype, from alcohol, is in the collection of Dr. C. P. Alexander, at Amherst, Massachusetts. Several females taken at the same time as the holotype were not designated paratypes and have apparently been discarded.

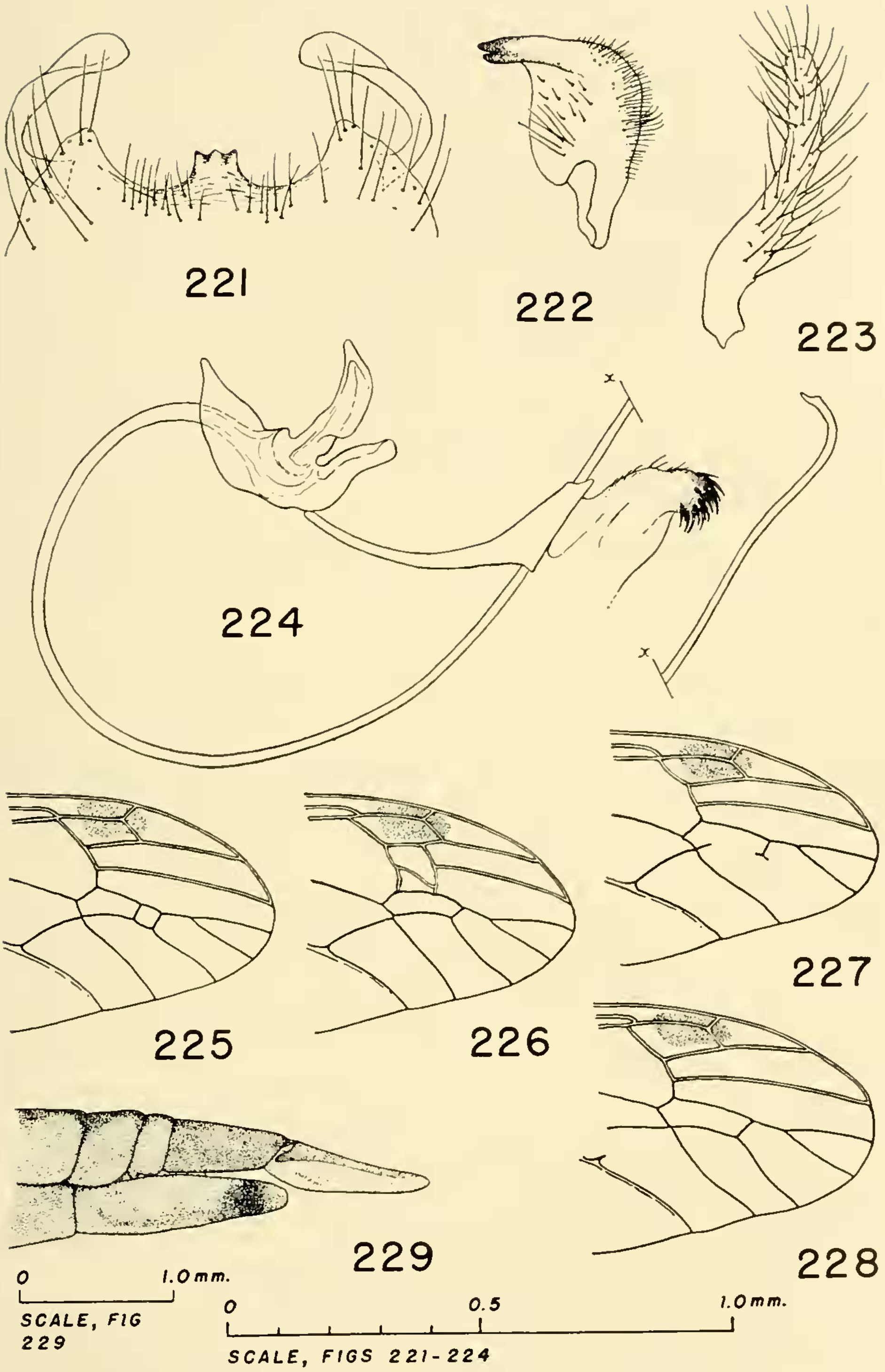
Diagnostic characteristics.—This species may be confused with *obscura*, *polita* sspp. and possibly with *johnsonella*. In the field, it may be distinguished from *polita* by its smaller size and distinct abdominal annulations; from *johnsonella* it differs in having the wings tinged with grayish brown instead of amber or golden brown. Field differentiation of *tridenticulata* from *obscura* should ordinarily not be attempted, for the reasons discussed under the latter species.

Male specimens of *tridenticulata* may be recognized readily by the configuration of the ninth tergum, with its characteristic three-toothed median lobe and slender tergal arms. In *polita cornuta* there is a tridentate median lobe, but the central tooth is invariably longer than the others and is often depressed; furthermore, the tergal arms and outer dististyles are conspicuously unlike those of *tridenticulata.* In female specimens of *tridenticulata,* the most darkly sclerotized part of the ovipositor is the subapical portion of the hypovalves, while in *obscura* females the tenth tergum is darkest. Females of all forms of *polita* have weaker abdominal annulations than *tridenticulata* or lack these altogether; in addition, the basal segments of the antennae of *polita* are paler than in *tridenticulata.*

Descriptive comments.—Dolichopeza tridenticulata, like *obscura,* is of a dusky brown color such that the flies are easily concealed in their shaded daytime haunts. However, where I have found the two species together, *tridenticulata* has usually been perceptibly lighter in over-all coloration. Particularly the thoracic dorsum is paler, being a dark reddish brown in *tridenticulata,* as described by Alexander, but dark brown in *obscura.* In the northern part of the range, *tridenticulata* is colored more nearly like *obscura.* In alcoholic collections of *tridenticulata* and *polita* sspp., flies often collected together in rocky ravine habitats, the former species may be recognized by the fact that the pleurotergite and a narrow portion of the other sclerites around the second spiracle are of the same shade of brown as the other sclerites of the thoracic pleura, while in *polita* these areas above the base of the haltere are darker than the rest of the pleura. This color difference is not evident in flies preserved dry.

Venational aberrations, especially those involving the media beyond its first fork, are widespread and very common in *tridenticulata.* Several of these were illustrated earlier (Figs. 40 through 48) in the discussion of intraspecific variation. These were regarded as locally inbred abnormalities. One specimen has been seen in which the m-cu cross-vein is broken and one segment of it strongly deflected (Fig. 228); in another, there is a spurious cross-vein in cell 1st M_2 (Fig. 225); and a third shows a most unusual abnormality of the branches of the radius (Fig. 226). Presence of the vein Sc_1 has been noted many times, and a few instances of failure of R_3 to reach the wing margin have been found.

Dolichopeza tridenticulata is one of the smaller species of *Oro-*



FIGS. 221-229. *Dolichopeza (Oropeza) tridenticulata;* 221—ninth tergum of male, 222—left inner dististyle of male, dorsal aspect, 223—left outer dististyle, dorsal aspect, 224—vesica, penis, adminiculum, adminicular rod and gonapophysis, left lateral aspect, 225-228—variations in wing venation, 229—terminal abdominal segments of female, left lateral aspect.

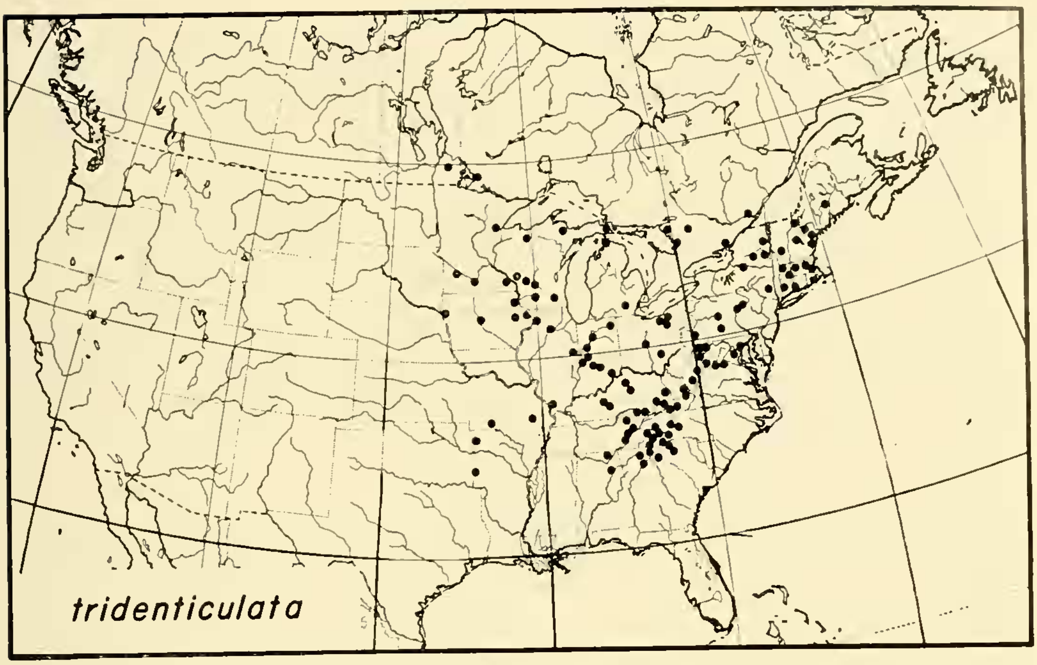
peza, nearly as small as *Dolichopeza* (*D.*) *americana.* Males average around 9 mm. in body length, with a 10.5 mm. wing, although they range from 7 to 10 mm. in length and have a variation in wing length from 8.8 to slightly over 12 mm. Females range in length of body from about 8 to 12.5 mm., their wings from 9 to 13 mm. The largest individuals of *tridenticulata* seen were from the Appalachian highlands of North Carolina and Virginia.

Variation in the profile of the medio-posterior margin of the ninth tergum of males consists primarily of the three widths of the subrectangular projection, as described earlier, under intraspecific variation. There are few localities in which *tridenticulata* has been taken where not all three of these forms are present. The commonest form, however, is that shown in Figure 221. The tergal arms are usually slightly flattened at their tips and may be somewhat widened (Fig. 221) or, less often, of uniform width throughout. The inner dististyle (Fig. 222) is very similar to that of *polita* sspp.

I have noticed that in many female specimens preserved either dry or in alcohol the cerci are deflected downward, so that the tips of the hypovalves are concealed. Why this happens in *tridenticulata* and not in *obscura, polita* or other species is not known. Antennae of females are about three-fifths as long as those of males taken at the same time and place.

Geographical distribution.—The geographical range of *tridenticulata* very closely approximates that of the three subspecies of *polita* combined. Collection records show that this species occurs from Maine westward to southeastern Manitoba, southwestward to the Ouachita Mountains, and southward along the Appalachian Mountains to northeastern Georgia. It must be much more widespread in southeastern Canada than present records indicate, and collections in western Arkansas, southern Missouri, and Iowa only sketchily outline its distribution along the edge of the plains. *Dolichopeza tridenticulata* will probably eventually be found in eastern Oklahoma and Kansas, possibly in Nebraska and eastern North and South Dakota. It may also occur in the Turtle Mountains of North Dakota and in the Black Hills of South Dakota. I would not expect it to range very far northwest across Canada beyond the presently known range.

Habitats.—In my experience, *tridenticulata* is primarily a rock gorge species; at least, it is in such habitats that I have found this species in the greatest numbers. Although I found it locally



MAP 10. Range of *Dolichopeza (Oropeza) tridenticulata* Alexander. Each spot represents one or more collections within a county (United States) or at a locality.

abundant in certain northern woodlands, it was never as common there as in many rocky Appalachian ravines and rock ledge gorges in Indiana and Ohio. The only published habitat data are from the mountainous region of western North Carolina, where Alexander (1941a: 297) found *tridenticulata* ". . . common under low earthen banks along road." In the vicinity of rocky ravines and boulder-strewn, forested mountainsides, *tridenticulata* is often taken away from the actual rocks, in such places as culverts, outhouses and other man-made shelters, open drain tiles, and beneath exposed tree roots, overhanging banks, or almost any other situation affording deep shade. They were frequent visitors in my tent, in Indiana, even when I had pitched it several hundred yards back from the rocky ravine where the flies were usually found by day. They always arrived during the night, in such cases, and frequently stayed until darkness fell again.

In the northern forests, *tridenticulata* was most often taken in or about small buildings, such as outhouses and picnic shelters. In some localities, it was found among granite boulders, where these were so arranged on a slope as to provide small, darkened crannies, here and there. In other localities, however, there were no rock outcrops seen, and the relief was so low that there could not have been any ravines; in one such place, *tridenticulata* was reared from a scanty growth of moss on a tree trunk.

Locally and in season, *tridenticulata* forms great swarms in shaded niches in the rocks, often in the company of *polita* and other species. At such times, one may easily capture hundreds of specimens. Because of this dense swarming, it seems to me a little unusual that prior to the beginning of this study only about 200 specimens of *tridenticulata* had been collected in all of North America, as far as I am able to tell. During periods of heaviest emergence in the gorges of southern Indiana, for example, it is possible to collect 200 individuals easily within ten minutes, and I have often stopped collecting only because I was satisfied that further examples of the species would not alter the characteristics of my sample.

Seasonal distribution.—Although there are collection records for all the summer months for practically all parts of the range, there is also good evidence of two annual peaks of emergence, in most localities. From Georgia and Arkansas northward to New England and southern Michigan and Minnesota, these peaks fall in June and August, locally about a week after the appearance of *polita.* In Parke County, Indiana, in 1953, the first individuals of *tridenticulata* were collected on 1 June, which was about two weeks after *americana* began to emerge, nine days after *polita cornuta,* four days after *walleyi* and *obscura,* and the same day as *carolus* first appeared. Peak numbers are reached about mid-June, in Indiana, and again between mid-August and early September. By 10 July, a few females were still present in the Parke County locality just mentioned. In another year, 28 August seemed almost the end of the late summer emergence of *tridenticulata* in nearby Owen County, Indiana. As in several other species, there appears to be a rather prolonged, single mid-summer period of emergence of adults of *tridenticulata* in northernmost United States and southern Canada. In northern Michigan, I found the peak of abundance to be about mid-July.

Individuals of the late summer generation are not conspicuously smaller than those taken in June.

Immature stages.—Average measurements of eggs from several females of *tridenticulata* are .65 by .30 mm. There is a well-developed terminal filament. Early instar larvae are unknown, but the third and fourth instars have been found in various relatively dry mosses. Larvae and many pupal skins were recovered from the moss *Dicranella heteromalla,* growing on the rather dry, upper surfaces of blocks of rock in wooded, rocky habitats in Ohio and Missouri. Pupae were obtained from *Tetraphis pellucida* where that moss was growing together with a powdery lichen, on a shaded sandstone cliff. The only specimens of *tridenticulata* known from southern Michigan are those reared from larvae collected from sparse tufts of the moss *Orthotrichum sordidum* that were growing in crevices of the bark of a tree, five feet above the ground. Larvae taken in the dry moss, *Hedwigia albicans*, and described as those of *obscura* (Alexander, 1920: 983) were found to be *tridenticulata*. The larva is very similar to that of the closely related *polita*, but is smaller and has the pleural hairs of the eighth abdominal segment irregularly arranged, leaving bare areas. These two species stand apart from all others in the genus, in that their larvae have the pleural hairs thickened and not arranged in circular groups.

Pupae of *tridenticulata* may be identified by the spiracular yoke, which is similar to that of *polita*. The yoke is broadly but shallowly emarginate, the emargination lacking the inner, rounded "shoulders" seen in *polita* and thus appearing very broadly V-shaped. In a sample of 16 pupae from Carter County, Missouri, all but three had a spiracular yoke as shown in Figure 122, the three having a shallower emargination. In this same group of pupae, 11 had no spinous processes on the fourth abdominal sternum and 5 had these developed to some degree. It was noted that in a few specimens the middle pair of spinous processes of the eighth sternum were barely close enough together to be regarded as of the usual form for the *obscura* group; such specimens, however, cause no difficulty in use of the key to pupae. The pupal stadium, under laboratory conditions, was six days.

Notes on distribution.—ALABAMA—Etowah County, 26 June; Madison County, 8 June. ARKANSAS—Polk County, 30 July; Washington County, 30 July. CONNECTICUT—Litchfield County, 9 July; New Haven County, 4 to 18 July. GEORGIA—Lumpkin County, 7 June; Stephens County, June; Towns County, 12 June; Union County, 23 May, 9-10 and 28 June. ILLINOIS—Carroll County, 7 July; Jackson County, 4 June; La Salle County, 7 July; Vermilion County, 13 June. INDIANA—Allen County, 10 July; Cass County, 8 June; Jefferson County, 2 to 23 June and 20 August; Montgomery County, 28 June; Monroe County, 23 June; Owen County, 4 to 7 and 18 to 27 June and 28 August; Parke County, 1 and 9 to 28 June, 10 July, and 11 to 30 August; Tippecanoe County, 20 June. IOWA—Boone County, 21 to 29 June; Clayton County, 8 July; Jackson County, 8 July; Linn County, 8 July; Woodbury County, 11 June. KENTUCKY—Barren County, 2 August; Bell County, 18 June; Edmonson

County, June (?); Franklin County, 23 June; Garrard County, 23 June; Letcher County, 3 July; Pike County, 3 July; Whitley County, 24 June. MAINE—Cumberland County, 13 August; Oxford County, 11 July; Penobscot County, 25 June to 5 July; York County, 1 July. MANITOBA—West Hawk Lake (near Rennie), 3-4 August. MARYLAND—Garrett County, 26 June; Montgomery County, 24 May to 28 June. MASSACHUSETTS—Berkshire County, 19 June; Franklin County, no date; Hampshire County, 1 July; Middlesex County, 11 July; Norfolk Co., 18 June. MICHIGAN—Cheboygan County, 5 to 30 July; Chippewa County, 13 July; Marquette County, 13 to 15 July; Washtenaw County, 14 May. MINNESOTA—Blue Earth County, 8 July; Carlton County, 6 August; Redwood County, 8 July; Winona County, 7 July. MISSOURI—Carter County, 6 June; Taney County, 10 to 20 June. NEW HAMPSHIRE—Coos County, 11 July; Grafton County, 14 July. NEW YORK—Essex Co., 1 July; Hamilton County, 12 July; Oneida County, 20 June and July; Ulster County, 28 June; Warren County, 2 July. NORTH CAROLINA—Buncombe County, 30 May; Burke County, 14 and 21 June, 1 July; Haywood County, 28 July; Macon County, 11 to 20 June; Swain County, 30 June; Transylvania County, 9 to 14 June; Yancey County, 26 May to 20 June, and 7 July. OHIO—Delaware County, May and 6 to 14 June; Geauga County, 17 July; Hocking County, 30 May and 6-7 June; Medina County, 4 July; Portage County, 24-25 June, 14 July, and 16 August. ONTARIO—Algonquin Park, 23 June and 10 August; Gananoque, 8 July; Go-Home Bay (Georgian Bay), 22 June; Kenora District (Lake of the Woods), 4 August; Pte. au Baril (Georgian Bay), 6 to 16 July and 15 August. PENNSYLVANIA—Centre County, 25-26 June and 9 July; Columbia County, 15 July; Huntington County, 9 July; Luzerne County, 27 June and 5 to 10 July; Westmoreland County, no date. QUEBEC—Rigaud, 25 June. SOUTH CAROLINA—Greenville County, 7 June and 1 September; Pickens County, 29 June. TENNESSEE—Bledsoe County, 26 June; Blount County, 20 May; Cumberland County, 25 June; Fentress County, 31 May to 20 July; Morgan County, 12 June; Sevier County, 7 to 23 June. VERMONT—Windsor County, 7 July. VIRGINIA—Fairfax County, 30 June and 5 September; Giles County, 1 June to 7 July and 20 July to 1 August; Rockingham County, 6 July; Shenandoah National Park, 28-29 June and 6 July; Smyth County, 20 June; Washington County, 20 June and 2 July; Wise County, 2 July. WEST VIRGINIA—Greenbrier County, 4 July; Pendleton County, 26-27 June;

Pocahontas County, 23 June and 5 July; Preston County, 25 June and 5 August; Randolph County, 5 July; Tucker County, 24-25 June and 6 August. WISCONSIN—Iron County, 6 August; Jefferson County, 21 June and 21 July; Juneau County, 6 July; Monroe County, 6 July; Sauk County, 5 July; Trempealeau County, June and 7 July.

Dolichopeza (*Oropeza*) *venosa* (Johnson)

Literature references.—*Oropeza venosa* Johnson. Johnson, 1909: 120, pl. 15 (hypopygium); Alexander, 1919: 930; Alexander, 1922b: 61; Alexander, 1924: 59-60; Alexander, 1925: 172; Johnson, 1925: 33; Alexander, 1928: 57; Leonard, 1928: 698; Alexander, 1929a: 236; Alexander, 1929b: 25; Alexander, 1930a: 212; Alexander, 1931a: 139.

Dolichopeza (*Oropeza*) *venosa* (Johnson). Alexander, 1936: 280; Alexander, 1942: 215, fig. 26J (hypopygium).

Original description.—"Front and rostrum yellow, vertex and occiput dark brown, palpi brown, antennae yellow, becoming fuscous beyond the first joint of the flagellum. Thorax yellowish with three broad, dark brown stripes, the dorsal stripe ending at the suture, the lateral stripes abbreviated anteriorly and interrupted at the suture; plurae subtranslucent; collar, scutellum, metanotum, a large spot on the center of the plurae, smaller spots at the base of the halteres and between the coxae dark brown. The black bands of the abdomen are united along the dorsal line, leaving a large yellow spot on the side of each segment. Halteres long, yellow; knobs dark brown. Legs light yellow, the tarsi yellowish white. Wings brownish hyaline; stigma and veins dark brown, the radial and cubital veins noticeably prominent, and the short median cubital cross-vein wanting. Genitalia brown, appendages black, style long, reaching the end of the penultimate segment, reddish, base black; appendages at the base of style acute, brown, tipped with black, margin deeply emarginate. Length, 10 mm."

Types.—Holotype male, Mt. Greylock (Berkshire County), Massachusetts, 15 June 1906, C. W. Johnson. Five paratypes, all males, from Brookline, Massachusetts, Moosehead Lake, Maine, Bartlett and Hanover, New Hampshire, and St. Johnsbury, Vermont. These six specimens are in the collection of the Museum of Comparative Zoology, Harvard University. Another male in this collection, from the type locality, 11 June 1906, but without a paratype label, is probably a paratype and the seventh specimen mentioned by Johnson (1909: 120).

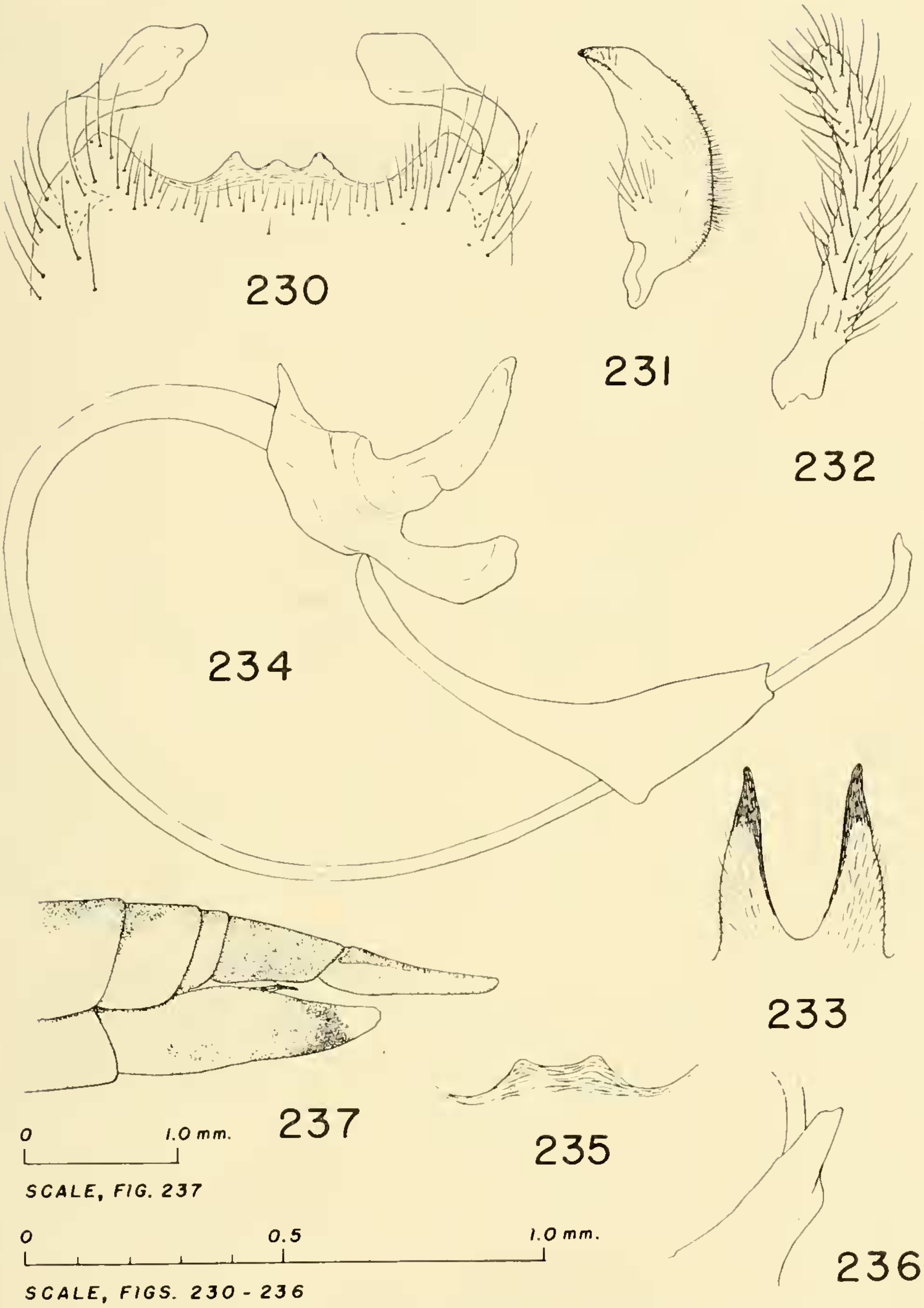
Diagnostic characteristics.—*Dolichopeza venosa* rather closely resembles both *carolus* and *subalbipes,* not only in general coloration but also in resting posture, but it differs from both in having yellowish instead of white tarsi and in lacking darkened tips on the femora and tibiae. Darker than *carolus* in over-all aspect, although like that species colored generally dark brown on tawny or dark buff, *venosa* is less contrastingly colored than subalbipes, which is more of a brownish black on yellowish buff. This coloration is particularly evident in the abdominal region. The prescutal stripes of *venosa* are more distinct than those of either *carolus* or *subalbipes.* This species is somewhat darker than the closely related *subvenosa,* a difference useful only in comparison of the two species.

Having long, acutely tipped, blackened gonapophyses (Fig. 233), males of *venosa* may be quickly separated from all other species except *subvenosa.* From that species, they may be distinguished by characteristics of the tergal arms and the adminiculum. The margin of the spatulate tip of the tergal arm in *venosa* is ordinarly angular (Fig. 230), but it is rather evenly curved in *subvenosa;* and *venosa* lacks the well-developed ventral spine found on the adminiculum of *subvenosa.* The inner dististyles of *venosa* (Fig. 231) are usually slender subapically but broadened in *subvenosa.*

Females of *venosa* may be recognized by the combination of the color characteristics described above with the intense subapical sclerotization of the hypovalves. They are separable from females of *subvenosa* on the basis of geographical range and, less reliably, by their darker color.

Descriptive comments.—Color variation in this species is particularly noticeable in the intensity of over-all coloration, certain individuals (usually males) appearing nearly as dark as *johnsonella* or even *obscura,* when seen from a distance of several inches. Coloration of the legs, especially of the femora, may be brown to yellowish brown, and the tarsi may vary from a very pale tan through yellowish white to almost white. The extent of the stigmal spot of the wing varies, being somewhat smaller in specimens from Wisconsin and Minnesota than elsewhere.

Venation in *Dolichopeza venosa* is very stable, as compared to some species in the *obscura* group. I have seen only three instances of an open cell 1st M_2 (discal cell) by loss of the medial cross-vein. One of these is a paratype, in which the abnormality was noted by Johnson. Half a dozen specimens seen had the veins M_{1+2} and M_3



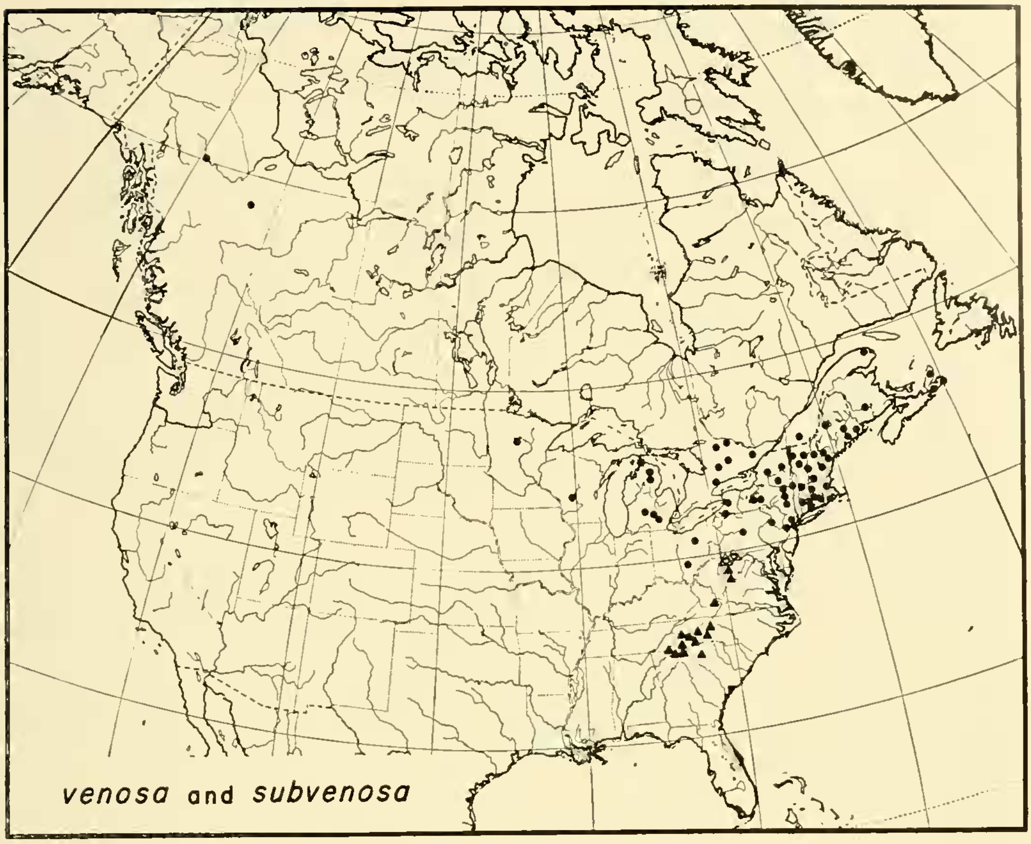
FIGS. 230-237. *Dolichopeza (Oropeza) venosa;* 230—ninth tergum of male, 231—left inner dististyle of male, dorsal aspect, 232—left outer dististyle, dorsal aspect, 233—gonapophyses, ventral aspect, 234—vesica, penis, adminiculum and adminicular rod, left lateral aspect, 235—variation in medio-posterior margin of ninth tergum of male, 236—adminiculum of male holotype, left lateral aspect, 237—terminal abdominal segments of female, left lateral aspect.

both joined with M_4 at the m-cu cross-vein; that is, the short length of M_{3+4} was missing. It is not unusual for the vein Sc_2 to join R_1 well beyond the origin of the radial sector. Johnson described the m-cu cross-vein as lacking; he referred to a short length of M_4 that results from the intersection of m-cu with M_4 instead of the junction of M_3 and M_4, but actually this disposition of the veins is not at all uncommon. A long, sloping medial cross-vein has been seen in two specimens, and a distally spurred cross-vein in only one.

Body length of males varies from 10 to 11.5 mm.; wings from 11.5 to 13 mm. Females measure 10 to 13 mm., their wings also from 10 to 13 mm. The smaller specimens are from Wisconsin and Minnesota, and the larger ones are from the central and northern Lower Peninsula of Michigan.

There is a great amount of variation in the profile of the ninth tergum of the males, although the medio-posterior projection ordinarily consists of a broad, three-lobed or three-pointed prominence. As in *subalbipes,* the central point or lobe is sometimes lost (Fig. 235). In a collection of 38 males of *venosa* from Eaton County, Michigan, I found 14 shapes of this part of the ninth tergum. Eighteen specimens resembled the form shown in Figure 230, two had two small median points, four lacked the central point but varied in the depth of the emargination, one had an accessory lateral lobe, and the other types were variations of the relative lengths of the central and lateral lobes. In this same group of 38 males, 27 had irregularly angular apical portions of the tergal arms, three had these rounded as in *subvenosa,* and eight were classed as intermediates. Rounded margins of the apical part of the tergal arm have also been seen in specimens from other parts of the range. Among the 38 males mentioned, 27 had inner dististyles somewhat suggestive of those of *subvenosa,* 11 as illustrated in Figure 231; 26 had no vestige of a spine on the adminiculum, but one had a spine about half as long as that found in the typical form of *subvenosa,* while 11 were of intermediate form. In specimens from New York, Connecticut and Massachusetts, I have seen various developments approaching the adminicular spine; in fact, the holotype of *venosa* has a low, rounded protuberance in the same position as that occupied by the spine in *subvenosa* (Fig. 236).

Geographical distribution.—Dolichopeza venosa occurs from Nova Scotia and the Gaspé Peninsula westward to Minnesota, northwestward to British Columbia and the Yukon, and southward



MAP 11. Range of *Dolichopeza (Oropeza) venosa* (Johnson) and *Dolichopeza (Oropeza) subvenosa* Alexander. Solid circles—*venosa;* solid triangles—*subvenosa;* circle within triangle—area where both forms occur. Each spot represents one or more collections within a county (United States) or at a locality.

to Ohio and Maryland. I have not seen the specimens from western Canada, which were collected by Dr. Alexander on his Alaskan trip in the summer of 1952, but I had rather expected that *venosa* ranged well northwest of Minnesota and northern Michigan, on the basis of the ecological distribution of the flies. The wide gap between the ranges of *venosa* and *subvenosa* that obscured their spatial relationships for many years was closed in the summer of 1958 with the discovery of both forms in northern West Virginia. My reasons for not regarding these two forms as subspecies have already been presented in the discussion of *subvenosa.*

Habitats.—This species has been found associated with the rocky ravine type of environment in some localities and elsewhere with cool, moist northern forests. Often, these habitats are combined. Deeply shaded crannies in a northern hardwood forest in Cheboygan County, Michigan, occupied mostly by *obscura,* were shared by *venosa;* and in Juneau County, Wisconsin, *venosa* was taken together with *polita,* under sandstone ledges. The *venosa-polita* association in a rocky habitat was found again in Eaton County, Michigan, where large numbers of both species were taken on the same date. In Centre County, Pennsylvania, *venosa* was swept from deep grasses at the edge of a hemlock-hardwood forest, where the forest opened rather abruptly into a mountaintop marsh. The habitat at Lake Itasca, Clearwater County, Minnesota, was in many ways similar to this. In general, forested areas, especially where these are also rocky, appear to be the most suitable environment for *venosa,* and much of the northeastern part of the United States and southeastern Canada comprises such an environment. Within this widespread habitat, *venosa* seems to be nowhere very abundant. Only once, in Eaton County, Michigan, have I seen aggregations of this species.

Seasonal distribution.—There are a few records for May, and most of the specimens are males, females appearing in the last days of that month. Most of the July records, on the other hand, are for females and are sporadic after the first week of the month. Records of June collections are by far the most numerous and point to a single early summer period of emergence, the peak coming in the last two weeks of June in most vicinities shown on the map, but several days earlier in the southern Ohio (Hocking County) locality.

Immature stages.—Eggs of this species, taken from a female of average size, measured about .79 by .32 mm. They have no terminal filament. Eggs laid on the nights of 31 May through 2 June began to hatch on 8 June, indicating the egg stadium to be about seven days. Four females, caged in the laboratory, produced over 300 eggs, each fly retaining several; accordingly, a female probably matures around 100 eggs. The larvae bear a striking resemblance to those of *subalbipes,* in that both species have the larger microscopic hairs of the dorsum arranged in irregular, interrupted and staggered or deflected transverse rows, which are short with the hairs long and densely set. This arrangement makes it virtually impossible to count the number of transverse ridges on any segment. Larvae were found in rather dry cushions of the moss *Plagiothecium roeseanum* that was growing on small amounts of soil trapped on a shaded sandstone cliff. It seems certain that this moss microhabitat was periodically well wetted by surface runoff and retained this moisture for many days. Nearby, on moist sand at the base of a cliff over which seepage water flowed, the moss *Leptobryum pyriforme* was growing, and there also larvae of *venosa* were found. The pupa is characterized by having conspicuous spinous processes on the posterior ring of the fourth abdominal sternum and by the spiracular yoke, the lobes of which are about twice as long as their basal width. It has been noted that the burrows prepared by the last instar larvae for pupation are unusually long, being about one and three-fourths to twice as long as the pupa. The duration of the pupal stadium is ordinarily six days; one female emerged on the eighth day but was abnormal and died before becoming completely freed of the pupal skin.

Notes on distribution.—BRITISH COLUMBIA—47 miles south of Fort Nelson, Alaska Highway milepost 253, 25 June. CONNECTICUT—Hartford County, 8 to 10 June; Litchfield County, 9 to 13 June; New Haven County, 29 June; Tolland County, 14 June; Windham County, 14 June. MAINE—Cumberland County, 1 July; Hancock County, 15 to 22 June; Oxford County, 11 July; Penobscot County, 25 June to 5 July; Piscataquis County, 11 July; Washington County, 15 July. MARYLAND—Garrett County, 28 June (*subvenosa* also here). MASSACHUSETTS—Berkshire County, 15 to 28 June; Hampshire County, 15 June; Norfolk County, 30 May and 18 June. MICHIGAN—Cheyboygan County, 22 to 30 June; Eaton County, 28 to 31 May; Livingston County, 11 June; Ogemaw County, 20 June; Oscoda County, 16 to 26 June; Washtenaw County, 4 June. MINNESOTA—Clearwater County, 16 June. NEW BRUNSWICK—Fredericton, 20 June. NEW HAMPSHIRE—Carroll County, 2 July; Cheshire County, 18 June; Coos County, 2 to 22 July; Grafton County, 5 July. NEW JERSEY—Bergen County, 1 to 15 June; Essex County, June; Morris County, July. NEW YORK—Albany County, 18 June; Cattaraugus County, 30 June; Cortland County, 21 July; Erie County, 4 to 23 June; Essex County, 16 June; Fulton County, 15 to 25 June; Greene County, June; Hamilton County, 17 to 23 June; Herkimer County, 9 June; Rensselaer County, mid-June; Tompkins County, 5 June. NOVA SCOTIA—Cape Breton County, 4 July; Richmond County, 1 July; Victoria County, 2 July. OHIO—Hocking County, 20 May; Portage County, 24 June. ONTARIO—Algonquin Park, 3 to 29 June; Burke Falls, 9 to 13 July; Gull Lake (Muskoka District), June; Orillia, 26 June to 2 July; Sand Lake (7 miles north of Gananoque, called "Sand Bay" on some maps), 2 July; Toronto, 17 June. PENNSYLVANIA—Centre County, 25 June; Luzerne County, 2 to 7 and 29 June. QUEBEC—Knowlton, 26 June; north shore Gaspé Peninsula, July. VERMONT—Caledonia County, 27 June; Chittenden County, 15 to 24 June; Washington County, 17 June. WEST VIR-

GINIA—Preston County, 25 June (*subvenosa* also here). WISCONSIN —Juneau County, 6 July. YUKON—Watson Lake, Alaska Highway milepost 632, 28-29 June.

Dolichopeza (*Oropeza*) *walleyi* (Alexander)

Literature references.—*Oropeza walleyi* Alexander. Alexander, 1931a: 139-140.

Dolichopeza (*Oropeza*) *walleyi* (Alexander). Alexander, 1936: 280; Alexander, 1940: 618; Alexander, 1941a: 297; Alexander, 1942: 216, fig. 26K (hypopygium); Rogers, 1942: 60; Rogers, 1949: 12; Whittaker, 1952: 34; Foote, 1956: 222.

As *Oropeza sayi* Johnson. Johnson, 1909: 118-119 (part); Alexander and McAtee, 1920: 393 (at least part); Rogers, 1930: 23; Rogers, 1933: 35, 49.

As *Oropeza similis* Johnson. Dickinson, 1932: 212, fig. 113 (wing).

As *Dolichopeza* (*Oropeza*) *dakota* Alexander. Alexander, 1944: 241-243 (new synonymy).

Original description.—"General coloration brownish yellow, the praescutum and scutum with clearly-defined brown areas; head gray; pleura yellowish white, without distinct markings; halteres with slightly infuscated knobs; legs pale brownish yellow; wings brownish yellow, the stigma brown; abdominal tergites obscure yellow with a brown median stripe, the lateral margins not darkened; male hypopygium with the gonapophyses large and conspicuous, the margins irregularly dentate. Male. Length, about 9-10 mm.; wing, 11-11.5 mm. Female. Length, 11-12 mm.; wing, 12 mm.

"Frontal prolongation of head pale yellow; palpi pale, the terminal segment suddenly blackened. Antennae (male) elongate, the basal three segments (male) or two segments (female) yellow, the remaining segments passing into brown, the basal enlargements a trifle darker. Head gray, with a dark median and posterior border, the occiput paler.

"Mesonotal praescutum brownish yellow, with three very distinct and clearly defined brown stripes; scutum similar, each lobe with two confluent dark brown areas; scutellum and postnotum pale brownish testaceous. Pleura yellowish white, without distinct dark markings, only the sternopleurite a little darkened. Halteres yellow at base, darkened outwardly, the knobs slightly infuscated. Legs with the coxae and trochanters yellow; remainder of legs pale brownish yellow. Wings brownish yellow, the costal region deeper yellow; stigma oval, conspicuous, brown; obliterative areas before the stigma and across the base of cell 1st M_2; veins brown.

"Abdominal tergites obscure yellow, with a dorso-median brown stripe, the lateral margins pale; sternites yellow, with a dark spot at the incisures, the outer segments more uniformly darkened. Male hypopygium with the caudal margin of the tergite with a broad V-shaped notch that is extended into a flattened flange bearing a small slender spine at base of notch; lateral arms of tergite expanded at tips into obtuse blades. Outer dististyle long and slender, the base not enlarged. Inner dististyle dilated, produced into a blackened beak that is unequally bidentate. Gonapophyses very large and conspicuous, yellow, the margins irregularly dentate."

Types.—Holotype male, Knowlton (Brome County), Quebec, 4 July 1929, G. S. Walley. Allotype, same locality and collector as holotype, 12 July 1929. Alexander (1931a: 140) listed in addition to the holotype and allotype "paratopotypes, 3 males and females, June 29-July 12, 1929 (G. S. Walley); paratypes, 2 males, Brookview, Rensselaer County, New York, June 14-21, 1923 (C. P. Alexander)." The holotype and one paratype of each sex are in the Canadian National Collection, in the care of the Department of Agriculture, Ottawa, Ontario. The allotype, one male paratopotype and a female specimen from Brookview, New York, 14 June 1923, labelled paratype, are in the collection of Dr. Alexander, in Amherst, Massachusetts. The present location of the other specimen or specimens from the type series is unknown to me.

Diagnostic characteristics.—Field recognition of *walleyi* is usually possible on the basis of a combination of appearance of the fly and the type of environment. When it rests by day in deeply shaded crannies beneath rock outcrops, together with species of the *obscura* group, *walleyi* may be easily recognized by its conspicuously paler thoracic pleura. From *carolus, subalbipes, venosa* and *subvenosa,* species with which it often occurs in leafy, low vegetation, *walleyi* is distinguished by its darker tarsi, which are never as pale as the darkest in those species. Occasionally, I have taken *walleyi* together with its nearer relatives, *sayi* and *dorsalis,* in swamp margins, and *similis,* in swampy woods. In such cases, sight recognition is difficult and not reliable; specimens should be captured before identification is attempted.

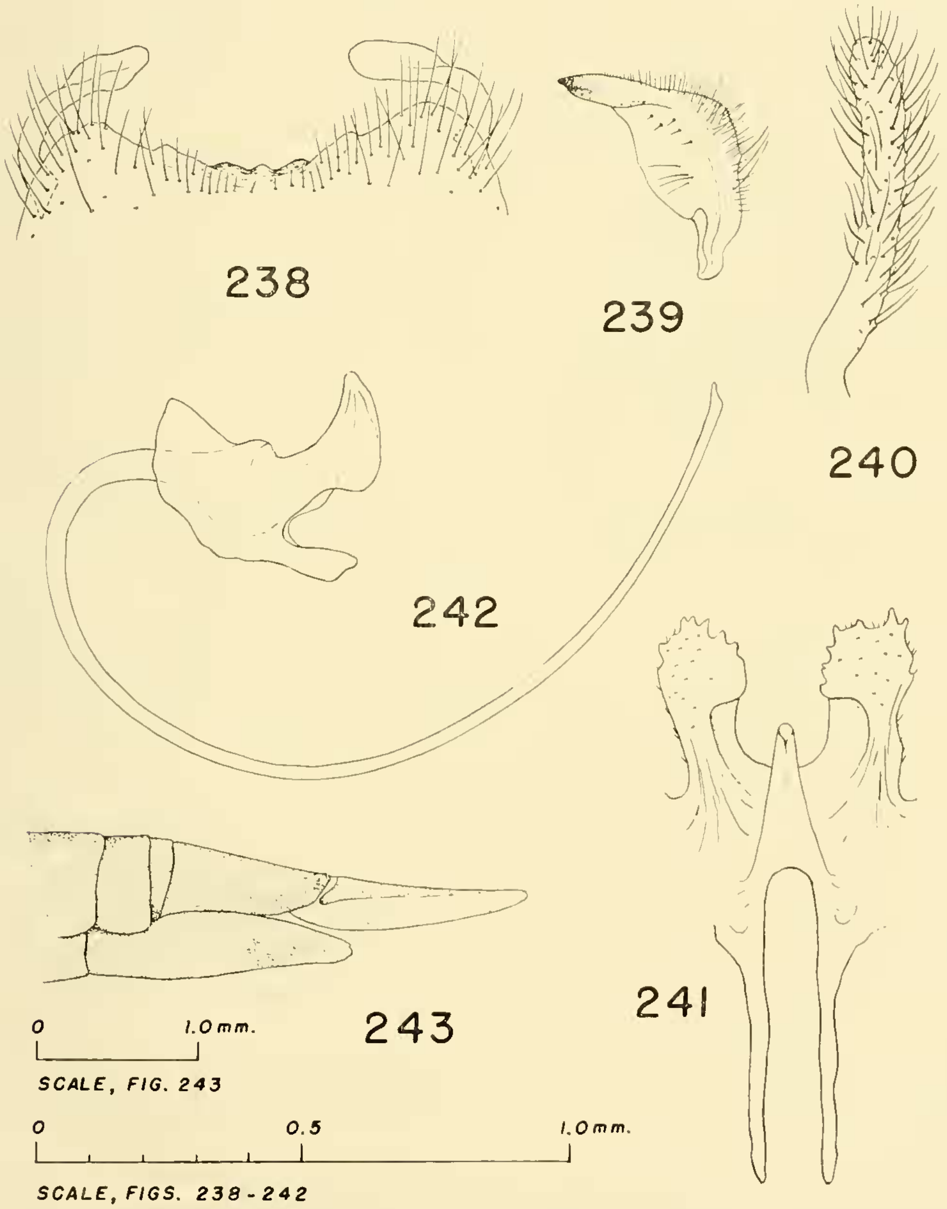
Males of *walleyi* may be readily identified by their gonapophyses, which are yellowish in color, flattened and flared at their tips and have irregularly toothed margins. Although in caudal, or ventral, aspect the gonapophyses of *walleyi* are very like those of *similis,* they do not have the heavy spine projecting from the inner face of each gonapophysis, as in *similis.* The gonapophyses in *sayi,* the only other species in which these structures resemble those of *walleyi,* are only slightly widened at their tips and have the margins entire.

Both males and females of *walleyi* may be recognized by their coloration, the yellowish body, yellowish brown legs and darkened thoracic dorsum together resembling, in a general way, only *sayi, dorsalis* and *similis.* The prescutal stripes in *walleyi* are, through most of the species' range, reddish brown, as compared with the nearly black stripes of *sayi* and the more brown but nearly obliterated stripes of *similis* and *dorsalis.* Where *walleyi* overlaps the range of *sayi,* the thoracic pleura are unmarked, or nearly so. There may be a slight darkening of the ventral part of the pre-episternum and mesothoracic meron, but this is never intense enough to be confused with the dark gray pleural markings of *sayi.* Outside the range of *sayi,* both sexes of *walleyi* take on color characteristics similar to those of *sayi,* so that females are most reliably identified by association with males.

Descriptive comments.—As pointed out earlier, in the discussion of intraspecific variation, the transition from unmarked to strongly marked thoracic pleura and the correlated transition from reddish brown to grayish brown thoracic stripes in *Dolichopeza walleyi* is not abrupt. Moving southward and westward from the center of the range of *sayi,* one first encounters noticeably marked or darkened populations of *walleyi* in Georgia, Tennessee, Indiana, Illinois, southern Minnesota and Saskatchewan. Specimens of *walleyi* collected south and west of the line indicated are increasingly strongly pigmented as their locality is farther from the line, so that the outermost populations, such as those from Florida, southern Missouri, eastern Kansas, western Iowa and the Black Hills of South Dakota, greatly resemble *sayi* in most details of coloration.

The single female specimen on which *Dolichopeza* (*Oropeza*) *dakota* is based (Alexander, 1944:241-243) has distinct grayish brown thoracic stripes and dark pleural markings; it has a seam of dark color along the cubitus and a rather darkly colored stigmal spot; and the subapical sclerotization of the hypovalves is quite dark. In all, this fly much more nearly resembles eastern *sayi* than it does the paler eastern form of *walleyi*. It was probably the intensity of the coloration that led Alexander to regard *dakota* as nearest to *venosa*. Having collected a large number of both sexes of the dark form of *walleyi* in the Black Hills and having compared females from among these with the holotype of *dakota*, I am convinced that *dakota* should be placed in the synonymy of *walleyi*.

Venational variation in *walleyi* includes the branching of M_3 together with M_{1+2} from the first fork of the media, so that M_3



FIGS. 238-243. *Dolichopeza (Oropeza) walleyi;* 238—ninth tergum of male, 239—left inner dististyle of male, dorsal aspect, 240—left outer dististyle, dorsal aspect, 241—gonapophyses, adminiculum and adminicular rods, dorsal aspect, 242—vesica and penis, 243—terminal abdominal segments of female, left lateral aspect.

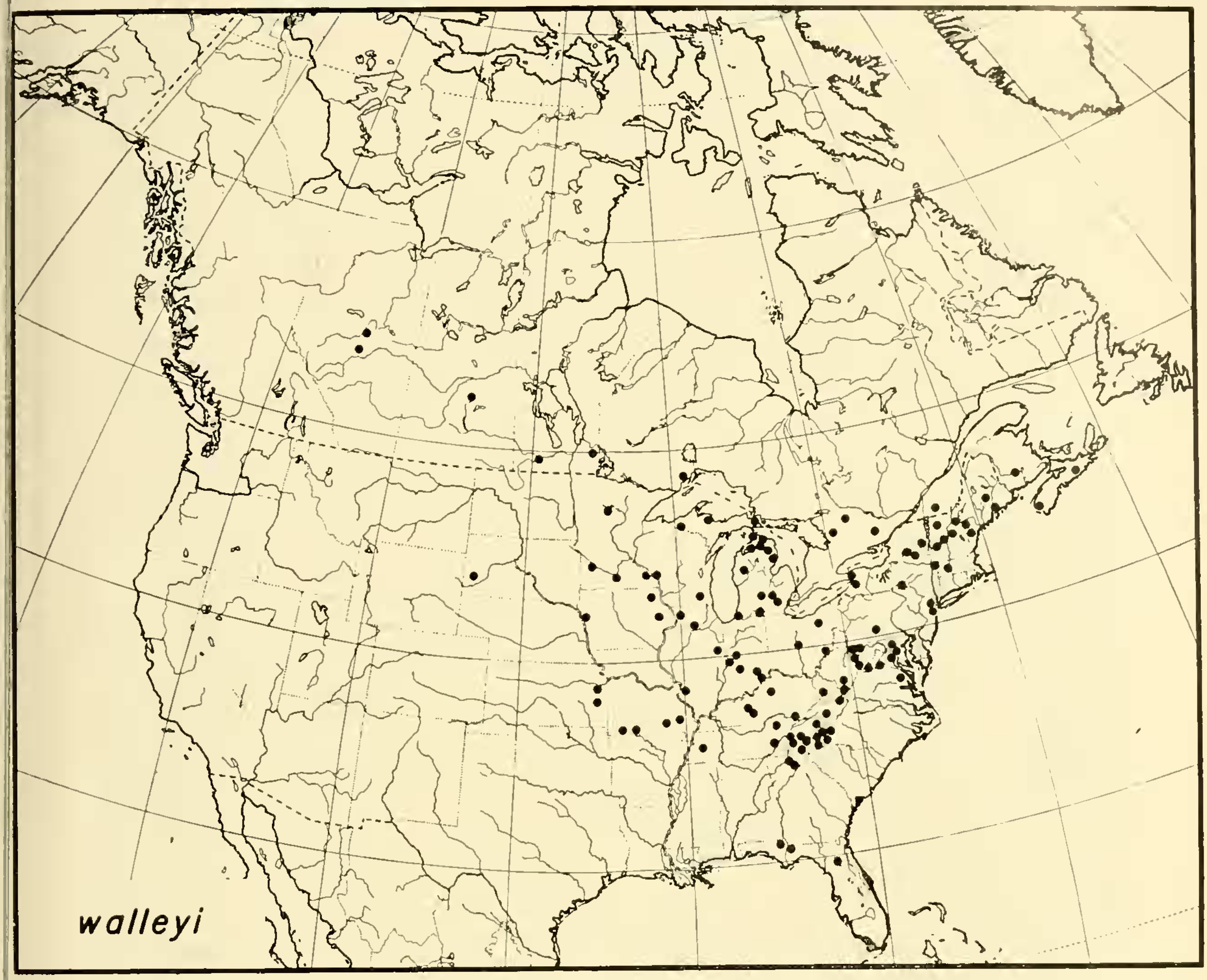
has no connection with M_4, a fragment of a spurious cross-vein in cell M_2, a nearly sessile cell M_1, and the vein Sc_1 sometimes present. Loss of the discal cell by absence of the medial cross-vein is not uncommon; in fact, the holotype of *walleyi* lacks the medial cross-vein in one wing and has it only faintly indicated in the other. In one specimen, the vein M_3 is basally interrupted, leaving the discal cell open for about half the distance between the junction of M_4 with m-cu and the medial cross-vein. In the vicinity of Ann Arbor, Michigan, there is a population in which individuals having macrotrichia in the outer cells of the wings are not uncommon. Occurrence of this condition in other parts of the range of the species has been noticed, but only in isolated cases.

Males of *walleyi* vary from 9 to slightly over 11 mm. in body length, and their wing measurements range from 9 to 12.5 mm. In the females, the wings are relatively shorter. Body lengths are from 11 to 14 mm., in the specimens examined, while the wings of these measured from about 11 to 13 mm. Larger specimens of both sexes were taken in June, and nearly all the small individuals were from August collections.

There seems to be no particular pattern to the toothed margin of the gonapophyses; that it, within a local population there are as many kinds of margins of gonapophyses as there are gonapophyses. This asymmetry is indicated in Figure 241. In *walleyi*, as in its near relative *similis*, the gonapophyses can be bent backward and ventrally from their bases, and in many specimens this has happened, apparently as a result of muscular action after the flies were placed in the cyanide jar. I have not seen the gonapophyses in such a position in living flies, so I do not know whether this action can be controlled.

In the shape of the tergal arms, there is also great variation (Figs. 64-66), and again there may be dissimilarity between the two tergal arms of one fly (Fig. 238). The depth to which the ninth tergum is cleft varies somewhat in living flies but also varies markedly in specimens preserved dry or on microscope slides, depending on the degree of compression or depression.

Geographical distribution.—The known range of *walleyi* is nearly as extensive as that of *dorsalis* in over-all length and is greater in breadth. The species ranges from Nova Scotia westward to central Alberta, southward to Florida and southwestward to the Ozark Mountains and eastern Kansas. I expect that *walleyi* will eventually be collected in eastern Nebraska and Oklahoma, in Alabama, Mis-



MAP 12. Range of *Dolichopeza (Oropeza) walleyi* (Alexander). Each spot represents one or more collections within a county (United States) or at a locality.

sissippi and Arkansas, and probably in the Turtle Mountains of North Dakota. Its range in Canada is only sketchily indicated; probably it is widespread in moist forests from the Great Lakes to Hudson Bay and northwestward to the Yukon, perhaps even into Alaska. Its occurrence in the Black Hills, where the population may be isolated, is discussed in the conclusions.

Habitats.—Like *obscura,* this species has appeared in a variety of general environments, and because of this wide range of habitat tolerance, *walleyi* is the second most numerous species of *Dolichopeza* in general collections. Common in the vicinity of rocky ravines and gorges, it is also found in many forest situations, where moisture conditions vary from wet to only slightly damp. In Turkey Run State Park, Parke County, Indiana, I regularly found *walleyi* together with the dusky-brown species of the *obscura* group in darkened crannies beneath outcropping ledges of sandstone. It was almost as commonly seen suspended among ferns and other leafy plants along the rims of the ravines, where *carolus* was usually found. In narrow ravines through the thick sandstone strata, where there was no accumulation of soil on the ravine floor, hence no trees, few or no low, herbaceous plants, and no mosses (the ravines are rather effectively scoured out by annual spring floods), *walleyi* was not found, although *polita cornuta, tridenticulata, americana* and occasionally some other species were present. This seems to be related to the fact that *walleyi* most often spends its immature stages in mosses that grow on the soil, while the other species mentioned usually pass their larval and pupal stages in mosses that grow on the sandstone cliffs. It is not unusual to collect *walleyi* in upland woods, especially early in the morning. Alexander (1941a: 297), for instance, reported it from rather dry woods at an elevation of 5200 feet, in western North Carolina. I found *walleyi* flitting about in low forest undergrowth atop Spruce Knob, Pendleton County, West Virginia, at approximately 4850 feet elevation, on a very foggy summer morning when the temperature stood at only 49°F. Rogers (1930: 23) records it from ". . . the course of a shaded, rocky, talus slope brook. . . ." in a cove at the edge of the Cumberland Plateau. In Florida, he reared adults from mosses on decayed logs and found other flies of this species among rank herbage on wet, shaded soil (Rogers, 1933: 49). In the southern Appalachian region, *Dolichopeza walleyi* has been found in forest and rocky ravine situations from the piedmont level up to nearly 6000 feet. Whittaker (1952: 34) took *walleyi* in a beech forest; and Rogers (unpublished notes) found it along brooks in wooded localities and about rock outcrops, in the vicinity of Mountain Lake, Giles County, Virginia. Several instances of this fly's having come to or into buildings near wooded areas have come to my attention; and while certain of these structures were picnic shelters and the like, others were buildings in which electric lights were operated at night, such as utility buildings in public campgrounds. Furthermore, there are several records of collection of *walleyi* in light traps, although rarely more than one specimen in any collection. This information, together with repeated daytime observations of *walleyi* spontaneously on the wing over low vegetation in moist woodlands, such as in floodplain forests, suggests that *walleyi* is not as strongly repelled by light as are several other species of *Dolichopeza*.

Occurrence of *walleyi* in swampy woods is not common, although I have occasionally taken it in such habitats together with *obscura* and *subalbipes,* and Rogers (1942:60) noted that the species was ". . . occasionally common in the lower flood-plain woods, birch-maple-elm and tamarack-sumac swamps, and along shaded stream banks; not taken in the marshes where the closely allied *D. sayi* is common, although the habitats of the two species overlap to some extent in the swamps." Only rarely have I taken *walleyi* in marshes; however, in South Dakota, this species was common, together with *dorsalis,* in a marsh of grasses, *Carex,* ferns and sparse, low willow scrub.

Seasonal distribution.—In seasonal distribution, there is again a close similarity between *obscura* and *walleyi,* in that it is somewhat problematical whether there are two annual generations in the area between the southernmost Gulf coast and Florida and northernmost United States and Canada. In his study of the Tipulidae of a southern Michigan locality, Rogers (1942: 60) states that *walleyi* was taken from 28 May to 9 July, in the years 1936 through 1938, with a few records for mid-August of 1938. He concluded that ". . . generally there is only a single generation a year in this region." From my collecting and rearing data, gathered in the same general area, I believe there are two annual generations, the second, however, without as well defined a peak of emergence as the first. In central and southern Indiana, where I have collected a great number of *Dolichopeza,* I have found rather well-marked June and August generations of *walleyi,* the spring peak of abundance coming early in June and the late summer peak around the third week of August. At Turkey Run State Park, Parke County, Indiana, in 1953, *walleyi* males first appeared on 28 May, five days after the first appearance of *polita cornuta* and about two weeks after the onset of emergence of *americana.* By 1 June, the numbers of *walleyi* were still at a low level, but the rise in population seemed to be steady. By 11 July, only a few females were left. The August emergence in this locality was found, in two different years, to be nearly completed by the last two or three days of that month. The Florida records are for March, April and June. In the vicinity of Washington, D. C., there appears to be a June generation and a second flight period from about the end of the third week of August extending into early September. In the northernmost parts of the United States and in the Canadian part of the range, there is a single generation annually, all the records being for June, July and early August.

Immature stages.—Eggs of *Dolichopeza walleyi* from a female from southern Michigan measured, on the average, .76 by .32 mm. There is no terminal filament. A single female may lay as many as 120 eggs, over a period of three or four nights. In the laboratory one female laid about 110 eggs in two nights but died before laying the few that remained. Hatching began seven days after the first eggs were laid, and many larvae had hatched out by the eighth day.

The larva of *Dolichopeza walleyi* resembles that of *sayi* and, to a lesser degree, that of *similis.* All these larvae have the microscopic hairs of the dorsum most abundant on the last two thoracic and first abdominal segments and on the seventh and eighth abdominal segments, while the transverse ridges are more faintly indicated on the intervening segments. These ridges, in *walleyi* and *sayi,* are readily perceptible, but in *similis* they are extremely faint. The rows of minute microscopic hairs interspersed among the transverse ridges are well defined, about six hairs in length, and about equally spaced in *walleyi,* while they are less well defined, composed of various numbers of hairs, and are crowded toward the transverse ridges in *sayi.*

A larva that I believe is almost certainly this species was described nearly 65 years ago by Hart (1895: 214-215), as a species of *Tipula.* The unknown larva, which Hart called Tipula larva "a," was taken from soil on the floodplain of Spoon River, Illinois. It was regarded as "probably young," very likely because of its small size as compared to other larvae of *Tipula.* Hart described it as follows: "Length 16 mm., diameter 1.5 mm.; grayish, covered with microscopic short dark brown pubescence denser on thorax and last segments, in transverse arrangement; folds very distinct, each slightly tranversely carinate and crested with darker pubescence, four folds on anterior divisions; each segment with the usual four setae, prothorax with several setae. Last segment with lower stigmatal teeth very small, triangularly black on upper surface; upper teeth slender, pointed, whitish, outer pair nearly twice as long as inner pair; a similar tooth anterior to each of the outer two, near the anterior margin of the segment; a blackish spot at the base of each upper tooth, and one below each stigmatal plate; anal prominence with four blunt tubercles about the anal opening." This is the same larva later designated as "*Tipula* sp. 6," by Malloch (1917: 202, pl. 31, figs. 6, 7).

In the shape of the spiracular yoke, *walleyi* pupae rather closely resemble those of *obscura,* but the two species may be readily distinguished by the characteristics of the pleural spinous processes (see key to pupae). Presence of well-developed spinous processes on the posterior ring of the fourth abdominal sternum will aid in recognition of pupae of *walleyi,* as these are found only in a few other species, notably *venosa, subvenosa* and *carolus.* Duration of the pupal stadium is six to seven days, under laboratory conditions. The occurrence of eulophid parasites in this species is described under the natural history of the pupae.

Bryophytes known to serve as microhabitats of the immature stages of *walleyi* are several mosses growing under widely differing moisture conditions. *Atrichum undulatum* is a coarse, often dry moss, usually growing on poor hilltop soil; yet the first immatures of *walleyi* seen were found in this moss. Also fairly dry was the thin mat of *Platygerium repens,* growing on the bark of a fallen tree. In contrast to these were the moist mosses *Amblystegium riparium* and *Mnium affine,* both on the soil at the margin of a temporary, shallow pool in hardwoods, in spring. Other mosses from which larvae or pupae of *walleyi* have been recovered are *Plagiothecium deplanatum, Entodon cladorrhizans,* and *Hypnum imponens,* all of intermediate degrees of moisture and all growing in rather thin mats on forest soil, near streams.

Notes on distribution.—ALBERTA—Bilby (about 30 miles west of Edmonton), 28 June; Fawcett (74 miles north-northwest of Edmonton), 20 June. FLORIDA—Alachua County, 29 March, April, and 3 June; Gadsden County, 5 April; Jackson County, 28 March to 18 April. GEORGIA—Lumpkin County, 7 June; Union County, 28 June. ILLINOIS—Carroll County, 7 July; La Salle County, 7 July; St. Clair County, 13 August; Vermilion County, 13 June. INDIANA—Jefferson County, 8-9 June and 30 July to 28 August; Jennings County, 3 August; Montgomery County, 28 June; Owen County, 6-7 and 18 to 26 June, and 3 and 28 August; Parke County, 28 May to 28 June, 11 July, and 28 to 30 August. IOWA—Linn County, 8 July; Winneshiek County, 8 July; Woodbury County, 11 June. KANSAS—Anderson County, 28 July; Douglas County, 25 May, 2 June, and 30 August. KENTUCKY—Barren County, 2 August; Edmonson County, June (?); Franklin County, 23 June; Whitley County, 24 June. MAINE—Cumberland County, 1 July; Hancock

County, 17 July; Oxford County, 11 July; Penobscot County, 25 June to 5 July. MANITOBA—Aweme (20 miles southeast of Brandon), 23 June; West Hawk Lake (near Rennie), 4 August. MARYLAND—District of Columbia, 29 August; Garrett County, 26 June; Montgomery County, 17 to 19 June and 25 August. MASSACHUSETTS—Hampshire County, 27 May. MICHIGAN—Antrim County, 2 July; Berrien County, 17-18 July; Cheboygan County, 22 June to 15 July; Chippewa County, 13 to 15 July; Eaton County, 30 August; Gogebic County, 27 July to 2 August; Iosco County, 28 August; Lake County, 12 June to 1 July; Livingston County, 28 May to 13 June and 14-15 August; Marquette County, 15 to 17 July; Oscoda County, 14 June; Otsego County, 3 July; Presque Isle County, 29 June; St. Joseph County, 12 August; Washtenaw County, 28 May to 29 June and 15 August. MINNESOTA—Blue Earth County, 8 July; Clearwater County, 11 to 17 July; Redwood County, 8 July; Winona County, 7 July. MISSOURI—Barry County, 29 July; Carter County, 6 June; Stoddard County, 31 May; Taney County, 10 June. NEW BRUNSWICK—Fredericton, 26 July. NEW HAMPSHIRE—Coos County, 2 to 11 July; Grafton County, 6 July. NEW JERSEY—Bergen County, 8 to 15 June; Essex County, June. NEW YORK—Broome County, 13 July; Erie County, 19 July; Essex County, 19 June; Hamilton County, 12 July; Herkimer County, 3 July; Niagara County, 23 to 28 June; Rensselaer County, 14 June. NORTH CAROLINA—Avery County, 14 June; Burke County, 14 June; Haywood County, no date; Macon County, 11 June; Swain County, 20 June; Transylvania County, 14 June; Yancey County, 9 to 22 June. NOVA SCOTIA—Halifax County, 5 August; Yarmouth County, 27 June. OHIO—Delaware County, 9 to 14 June; Portage County, 24 June and 14 July; Washington County, 19 June. ONTARIO—Algonquin Park, 26 June to 3 July; Burke Falls, 13 July; Sand Lake (7 miles north of Gananoque, called "Sand Bay" on some maps), 5 July; Thunder Bay (Lake Superior), 9 July. PENNSYLVANIA—Huntington County, 9 July. QUEBEC—Knowlton, 29 June to 12 July. SASKATCHEWAN—Stony Lake (near Humboldt), 5 June. SOUTH DAKOTA—Pennington County (Black Hills), 11 and 23-24 July. TENNESSEE—Blount County, 15 to 17 June; Cumberland County, 25 June; Fentress County, 13 August; Haywood County, 25 May; Knox County, 28 May; Sevier County, 7 to 18 June; Washington County, 30 August. VERMONT—Lamoille County, 17 June; Orange County, 11 July; Rutland County, 12 July. VIRGINIA—Fairfax County, 24 June and 5 September; Giles County, 7 to 22 June and

26 August; New Kent County, 31 May; Rappahannock County, 30 June; Rockingham County, 6 July; Washington County, 18 August. WEST VIRGINIA—Greenbrier County, 4 July; Mingo County, 3 July; Pendleton County, 27 June; Pocahontas County, 23 June; Preston County, 25 June; Tucker County, 24-25 June. WISCONSIN—Jefferson County, 21 June; Trempealeau County, 7 July.

SUMMARY AND CONCLUSIONS

These laboratory and field studies of *Dolichopeza* point out certain problems involving groups of several species and in addition allow a few generalizations that apply equally to all North American species. It has seemed best to discuss these here, in conclusion, following presentation of the detailed data relating to each species.

Taxonomic categories.—It was one of the purposes of this investigation to try to determine what biological species are represented by the various described forms. To do this, it is first necessary to decide what is meant by a species. I visualize a species of *Dolichopeza* as a series of populations of morphologically similar, actually or potentially interbreeding individuals, effectively reproductively isolated from other such series of populations, having a certain geographic range and ecological distribution, and maintaining these characteristics through a span of time in the evolutionary sense.

A satisfactory interpretation of the diversity of structure (and other characters) found in North American *Dolichopeza* requires the examination of large numbers of individuals. Study of one or two specimens here and a few there places undue emphasis on their differences, but when more nearly the full spectrum of variation within a genus can be seen, similarities are emphasized and natural groups can be separated and ranked with perhaps less ease but much more confidence. Individual variants, locally inbred mutations, and geographic races are more likely to fall into their proper taxonomic places when viewed against the background of the entire range of variation of their species. Application of this point of view, I believe, can lead equally to "splitting" or "lumping" of older taxonomic categories.

In judging where specific boundaries should be drawn in *Dolichopeza* (for no matter how ideal his definition of a species, the taxonomist must in the end judge specimens and assign them to specific categories according to his opinion), I have relied heavily on comparative morphology. Individuals having essentially the same appearance (allowance being made for sexual differences) are presumed to have very similar genotypes and are further presumed to belong to an interbreeding population, if collected in one locality, or to potentially interbreeding populations, if collected in scattered localities. Specific boundaries have been further clarified by the evidence of reproductive isolation among the species recognized. Of the more than 11,000 flies examined, not one was regarded as a hybrid of any two species. Furthermore, among hundreds of mating pairs observed in the field and in the laboratory, none was ever found to involve male and female of different species. Although species of *Dolichopeza* repeatedly come into close proximity under natural conditions and were even caged together in the laboratory, no indication has been found of exchange of genetic materials between species.

Minor variations having more or less random distribution within a species (such as small differences in shape of ninth tergum or minor shifts in position of wing veins), as well as somewhat more striking variations of localized occurrence (for example, locally inbred venational peculiarities) and seasonal size differences, have required no taxonomic recognition. Even in certain cases when variation could be correlated with geographical distribution, taxonomic recognition seemed not to be indicated, such as the instance of *Dolichopeza dakota*, which was judged to be only an extreme in the clinal distribution of color in *D. walleyi*.

Where it has appeared clear that there is gene flow between morphologically distinct forms that are allopatric except for relatively narrow zones of overlap, these forms have been regarded as subspecies, the single example being in *Dolichopeza polita*. Across the zone of contact between the central and eastern forms of this species, in the central and southern Appalachian Mountains, there is concordant change in all the characters that have been found to vary geographically—structure of hypopygium, degree of luster of the thorax, and details of coloration. Individuals of the respective forms from outside the zone of intergradation are in all cases taxonomically distinct and readily separable, but within that zone both forms may occur, together with varying percentages of intermediates. Similar intergradation occurs at the only known locality where the western and central forms meet.

If degree of difference between sympatric species can be taken as a fair indication of the relationship of allopatric forms in the same genus, some support for regarding the subdivisions of *polita* as subspecies can be gained from the fact that a series of unusual characters common to these very similar forms are not found in any of the other species. Among these are the reversed relative sizes of males and females, the basal enlargement and pointed tip of the outer dististyles in the males, the coiled tracheal connection in the pupa, and the abbreviated terminal filament of the egg.

A series of collections made at Nelson Ledges State Park, Portage County, Ohio, in three different years, included many mating pairs of the eastern and central forms yet never a pair involving both forms and never an individual that could be regarded as an intergrade between the two. Notwithstanding the fact that these two forms intergrade in a zone extending from nearby points in Ohio to eastern Tennessee, in this one locality they may have achieved a specific level of reproductive isolation. Where the eastern form enters Michigan and Wisconsin it is wholly distinct, no areas of contact with the other races having been discovered in that region. An attempt to explain these relationships follows below, under the heading, species formation.

When morphologically distinct forms have allopatric but contiguous geographical distributions yet show no clear evidence of intergradation along the line of contact, as in the case of *Dolichopeza venosa* and *subvenosa*, the forms have been regarded as full species. That these two forms do come into contact has only recently been established, and there is so far no indication of interbreeding, except for the very sporadic occurrence of certain modified characters of each form within the range of the other, as discussed earlier.

In the case of *subalbipes*, where there are two forms with regard to one character only (tergal arm), with continuous gradation in other characters, it seems reasonable at this time to recognize only one species.

Isolating mechanisms.—In *Dolichopeza*, closely related species often have nearly identical geographical ranges and are often the most closely associated ecologically. There is some very general environmental segregation, yet adults of as many as half a dozen species may not infrequently occur so close together in their daytime resting places that they come into physical contact, especially when in swarming flight following some disturbance. Larvae of two or three species are occasionally found within a patch of a single species of moss no larger than the palm of one's hand. Under such circumstances, it is difficult to imagine how these species might be separated by any environmental barriers. Of course, isolation in any stage but the adult is irrelevant to the problem of interspecific isolation; we are concerned here with reproductive isolation, which must be complete in the case of sympatric sibling species in order for them to retain their identity. Reproductive isolation ordinarily occurs because males and females of different species are not attracted to each other and thus do not mate at all. In other instances in which mating between species does occur, either there may be no fertilization or, if fertilization is accomplished, the offspring may be either inviable or sterile. The composition of mating pairs mentioned earlier suggests that in *Dolichopeza* the first of these possibilities is the rule.

Differences in size of individuals and in relative proportions of genitalic structures could probably account for a certain amount of isolation between species in the same habitat, as between *similis* and *dorsalis,* but in most cases I cannot see any structural barriers to interspecific matings. As pointed out earlier, there is no "lock and key" arrangement in copulation. The fact that peaks of emergence of adults do not coincide may provide a degree of reproductive isolation, but there is still such great overlap in the seasons of emergence of the various species in any locality that this would scarcely seem to be an effective isolating mechanism. It has been noted that mating in *americana* often takes place by day, while species of *Oropeza* ordinarily mate at night. This, however, fails to explain isolation among the closely related species of *Oropeza,* which is really the problem at hand.

That species of *Dolichopeza* carry on mating and other activities primarily in the hours of darkness may still have some bearing on the means of isolation. It seems not unlikely that the process by which males and females of one species are attracted or brought together might also serve to repel all other species. That is, each species might be characterized by a particular odor, allowing males to detect females of their own species and distinguish them readily from all others. Flies caged in the laboratory, as well as those congregated in natural resting sites, occasionally exhibit diurnal mating but in general ignore one another, by daylight, unless they come into bodily contact. It is possible that matings begun in daylight hours are merely the result of reflex reactions following appropriate but accidental contacts and that the stimulus of daylight causing resting behavior ordinarily overcomes any stimulus for other activity short of actual contact.

Population control.—Potentially, a local population of any species of *Dolichopeza* could saturate its environment in a short while; however, it is my general impression that, in areas where I have made observations over a period of several years, such local populations have remained about the same. It is, of course, difficult to discover whether populations of various species of *Dolichopeza* are in the long run increasing or decreasing. It seems not unreasonable to assume that, although each species is constantly striving to increase, any particular population fluctuates from year to year according to environmental factors and that net gains during a favorable year may be wholly or in part cancelled by losses in an unfavorable one.

The number of individuals of a species in a local population (and it is both reasonable and convenient to think of species of *Dolichopeza* in terms of many localized, partially isolated populations) is derived from an interaction of the species' potential rate of reproduction and the effects of the environment. Each female reaching the adult stage is presumably capable of depositing 100 to 120 eggs. The longevity of ovipositing females needs to be taken into account, although most of the eggs seem to be laid within three or four days of the time of emergence. One must also consider, in connection with the species' reproductive potential, the number of generations per year. Assuming for simplicity that there is but one generation each year and that the population shows no measurable increase from year to year, it may be seen that 98 percent or more of the potential offspring of each generation are lost before the next. What is the fate of all these individuals?

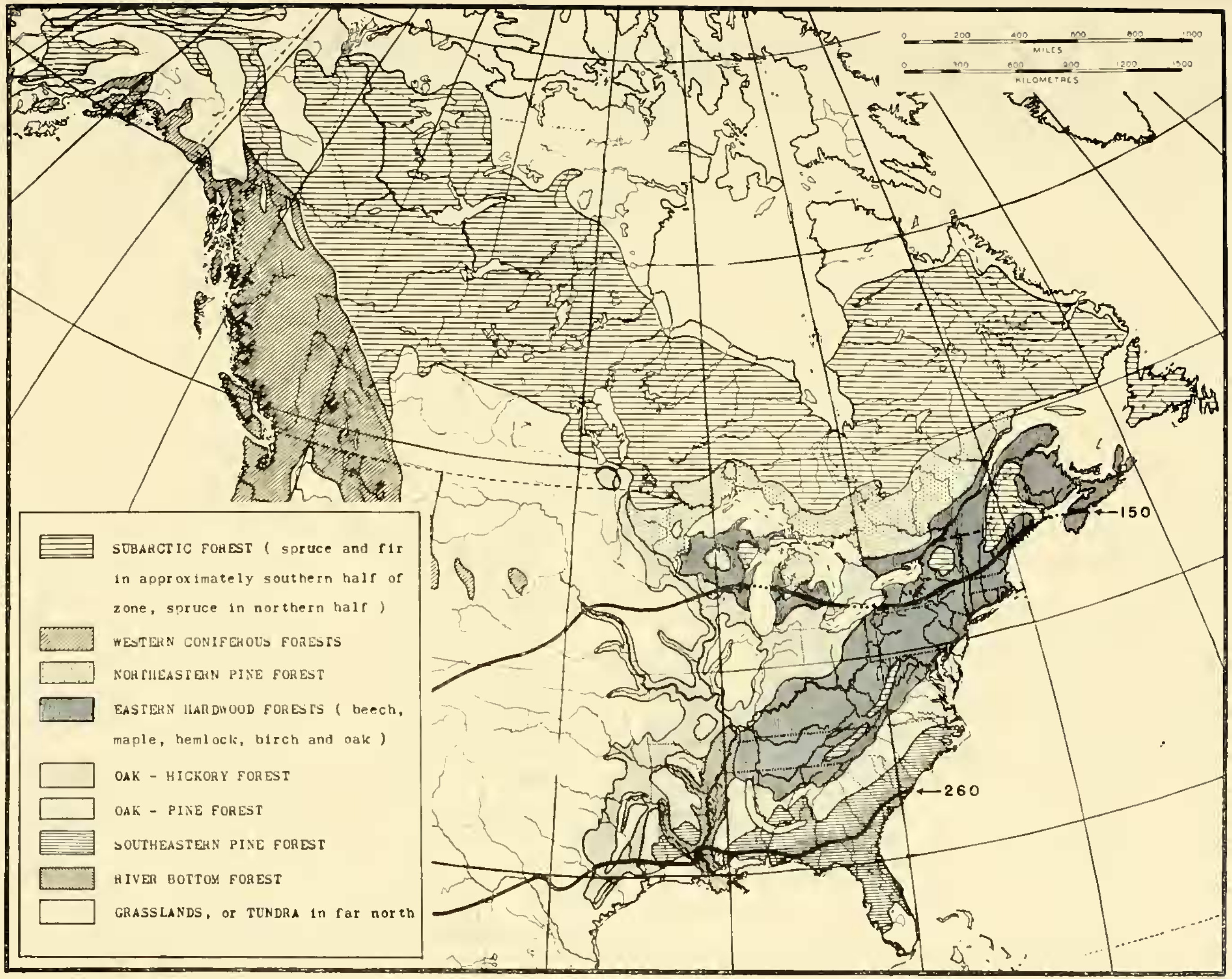
Due probably to the method of fertilization, as many as a third of the eggs of one female have been observed, in the laboratory, not to hatch and are assumed to have been infertile. The proportion of such losses in nature cannot easily be estimated, but it is difficult to imagine biological perpetuation of such inefficiency. Mortality in the larval stages has been found to result from predation, parasitism, disease, and the effects of severe adverse weather, such as excessive rainfall, drouth, or extreme temperatures. In the laboratory, many individuals died in the pupal stage, from predation, parasitism and unknown causes. Of the adults that survive the hazards of emergence from the pupal skin, certainly many do not reproduce, again by reason of predation, disease, weather or accidents of one sort or another.

Other environmental limitations that need to be considered are availability and quality of food, space in the habitat, and competition—both among individuals of the same species and among the various species inhabiting the same general environment—for food and space.

Competition.—There is no evidence of competition among species of *Dolichopeza*, either from records of changes in species composition in various localized environments, over the years, or from field observations of many larvae and numerous large aggregations of adults. In habitats where a number of species are present, there seems always to be more than enough of both the bryophyte microhabitats for the immature stages and shaded resting places for the adults. As mentioned earlier, the moss or liverwort habitat is almost never fed upon by the larvae sufficiently to cause readily visible damage. Even though larvae of three species may be feeding together in one kind of moss, they rarely come into contact with each other because of the abundance of the moss (which is at once their food and shelter) and because individuals were initially spaced within the habitat as a result of the method of oviposition.

It might be theorized that, in time, one species or another, by being more exactly adapted to the environment, would so gain in numbers as to force the others out through competition. However, it seems probable that fluctuations in the environment favor first one species and then another and that, because of the irregular geographical distribution of such fluctuations, a species may gain temporary predominance in one locality but fall to low numbers in another, in an ever-changing pattern. As Ross (1957: 127) points out, "Because no two species are exactly alike genetically and therefore physiologically, each species should theoretically have an ecological optimum slightly different from all other species. It follows that, in cases of multiple occupancy of a niche [by species of the same genus], each species will tend to become abundant at a time or place different from the other species."

It appears that numbers of *Dolichopeza* are so reduced by predation, parasitism, disease and rigors of the physical environment that competition, except perhaps at the level of the individual, never comes into play as a force in population control. Absence of competition, either among species of *Dolichopeza* or between this genus and species of *Liogma, Tipula,* etc., living in the same habitat, would furthermore seem to be an important factor in the ability of several species of *Dolichopeza* to occupy one and the same ecological niche.



MAP 13. Some ecological factors influencing the distribution of *Dolichopeza* in North America. Shading indicates forested regions; heavy lines are isophenes of average length of frost-free period, in number of days indicated.

Geographical distribution.—In a general way, the pattern of distribution of the genus *Dolichopeza* in North America corresponds with that of the forests in the eastern and subarctic regions of the continent (Map 13). Within this vast area, there are many recognized forest types, and one species of *Dolichopeza* may range through several of these. Accordingly, the composition of the forest does not appear as important to the distribution of these crane flies as the general effect that the presence of forest trees has upon the microhabitats required by the flies and their larvae. So similar are the ecological needs of species in various groups of *Dolichopeza* that the geographical ranges of certain of them nearly coincide. In fact, if the known ranges of all species were outlined on one map, it would be seen that the area including roughly the Great Lakes basin and the northern Appalachian Mountains is inhabited by twelve of the fifteen recognized species. A series of zones drawn around this central area would include diminishing numbers of species toward the periphery of the range of the genus. Even near the periphery, however, any habitat suitable for one species is likely to support two or more. Thus, in eastern Kansas, near the western limit of the forests, were found *obscura, polita pratti* and *walleyi;* of two specimens of *Dolichopeza* taken in the Ouachita Mountains on the border between Arkansas and Oklahoma, one was *johnsonella* and the other *tridenticulata;* and in western Alberta, near the Continental Divide, over which no species seems to have passed, at that latitude, were found *americana, dorsalis, obscura* and *walleyi.* On the other hand, the range of every species must naturally come to an end somewhere, and I certainly do not suppose that, at the actual outer limits of the range of the genus, at least two species will always be found existing in the same habitats. Beyond the region of generally satisfactory habitats, perhaps one species here and another there may be pioneering, as it were, various marginal environments. Each species probably expands its range during years in which its over-all environment has been most nearly optimum, only to be thrown back in unfavorable years, perhaps here and there holding some of the gained ground in spite of adversity.

Although there seem to be altogether favorable habitats for *Dolichopeza* in the luxuriant forests of the Cascade Range of Oregon and Washington, the genus has apparently been prevented from westward expansion at this latitude by the Great Plains. By the route of the subarctic forest, several species occurring in eastern

North America have spread northwestward across Canada toward Alaska, bypassing the treeless plains and even moving a little way southward again, below the eastern slopes of the Rocky Mountains, following an extension of the boreal spruce-fir forest. So far as is known, however, these species have not penetrated the western coniferous forest (lodgepole pine, western yellow pine, etc.) and remain east and north of the Continental Divide.

If the plains are such an effective barrier to the spread of *Dolichopeza,* how does the genus happen to be represented by at least three species in the isolated Black Hills of South Dakota? One might at first suspect a connection to the main eastern range by way of the valleys of the Missouri and Cheyenne rivers, yet there is a 300-mile gap between the Black Hills and the northwestern extremity of oak-hickory forest in the Missouri Valley. The species composition of the Black Hills group (*americana, dorsalis* and *walleyi*) suggests that the group's geographic affinities are with the area to the north; however, once more the continuity of habitats is widely broken. It seems that the Black Hills are in fact wholly isolated and that species of *Dolichopeza* now living there have no connections whatsoever with their main eastern and northern ranges. In order to account for this distribution, it is necessary to visualize that at the time of maximum extent of the last (Wisconsin) continental glaciation, *Dolichopeza* occupied a forest that grew all along the ice front, which is to say from the Rocky Mountains along the Missouri and Ohio rivers to the Appalachian Mountains. As the ice withdrew northward, followed by the boreal forest, a remnant of that forest, into which elements of the Rocky Mountain forest had become introduced, was left behind, where, because of the cooler climate and higher rainfall in the isolated mountains, it withstood the encroachment of drier forests and eventually of grasslands. If this is how species of *Dolichopeza* came to be in the Black Hills today, what accounts for their not having visibly changed from the parent stocks in their ten thousand years or more of isolation?

The species involved all have unusually extensive ranges, spanning approximately thirty degrees of latitude and including habitats from near sea level to more than 6000 feet elevation, distributed in a great arc nearly 4000 miles long from southeastern United States to northwestern Canada and Alaska. Not one of them, however, has differentiated into geographic races in response to the great ecological diversity encountered within its range. This suggests that these species have a high degree of adaptability and that such changes in genetic constitution as have been necessary to adapt physiology to environment have been so small that they have not become manifest in the phenotypes. It is thus not unusual that species of such constitution have remained essentially unchanged through ten thousand years in isolation, for surely the environment has changed less in the Black Hills during that span of time than it changes today over the length and breadth of the described range.

Seasonal distribution.—The geographic range of the genus *Dolichopeza* in North America may be divided into three major zones with respect to seasonal distribution. These are: (1) Florida and the extreme southern Gulf Coastal Plain, where emergence of adults may occur in almost any month of the year; (2) a broad middle belt extending from Florida and the Gulf Coast area northward to New England, central Michigan and southern Wisconsin and Minnesota, in which there are normally two annual appearances of adults, falling roughly in June and August; and (3) a northern zone, in which one annual flight period, usually during late June and July, is the rule. As this pattern of seasonal occurrence correlates in general with latitude and since cold weather is known to inhibit feeding activities of the larvae, temperature appears to be the chief factor involved.

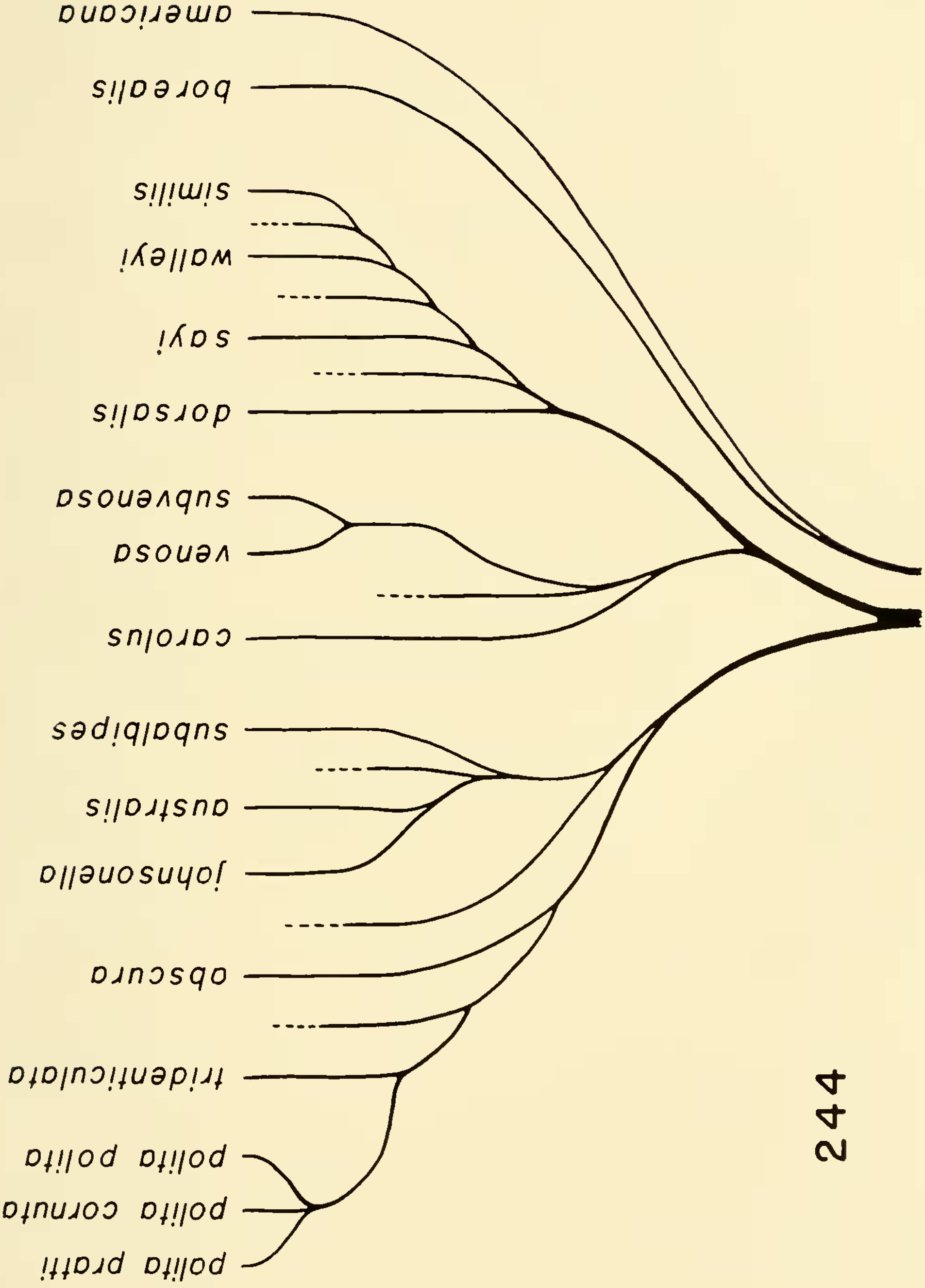
Duration of the frost-free season may perhaps be taken as a measure of the time available for larval feeding and growth, hence of the potential production of adults. If contours are drawn upon a map, connecting points of equal average duration of frost-free period, two of these contours very closely approximate the zonal boundaries of seasonal distribution in *Dolichopeza.* The boundary between the southern and middle zones falls near the 260-day contour (Map 13), and the middle and northern zones are separated more or less along the 150-day contour. On the average, the last frost of spring along the southern contour is in early March and the first frost of fall in late November or early December. Along the northern contour, the last spring frost is usually around mid-May, while the first in autumn comes in early October. Within the broad middle zone, there is thus an average feeding and growing season of somewhat over 200 days. Rearing of *Dolichopeza sayi* in southern Michigan indicates (Fig. 99) that about 70 days are required for the development of one generation. Accordingly, supposing that occurrence of frost brought larval feeding and growth to a halt, there would be only sufficient frost-free days at that latitude to produce two generations of *sayi* in an average year. It is furthermore not unlikely that when frosts come early in the fall or persist late in spring, only one generation may be produced, as in the northern zone. Depending on local micro-climates, there may result a partial second generation, which would perhaps account for the fact that, in the northern part of the middle zone, the number of adults in the late summer generation is often conspicuously smaller than the number seen at the same locality during the spring emergence.

Species formation.—Dolichopeza is probably a very old genus. The present day tipuline genera *Brachypremna, Tipula, Ctenophora* and possibly *Nephrotoma,* as well as nearly twenty modern genera of the Limoniinae, were already differentiated in Oligocene time (see Alexander, 1931d) and are represented as fossils in deposits of that epoch in Europe and North America, especially in the Baltic amber. As *Dolichopeza* is regarded as a rather primitive genus among the Tipulinae, it quite possibly was differentiated prior to the Oligocene and spread widely into North America from Asia, at a time when a low, forested land connection existed between the two continents in the region of Alaska.

There appear to have been three, possibly as many as five, separate introductions: one or two each of *Dolichopeza* s. s. and *Oropeza* and one of *Megistomastix*, a West Indian subgenus that seems not to have been derived from either *Oropeza* or typical *Dolichopeza.* Given the forty million years or so, suggested above, to diversify in North America, these originally introduced species could easily have given rise to the present fauna, notwithstanding their apparently slow rate of evolutionary change. Despite the evident ability of species of *Dolichopeza* to adapt to diverse general environments, it seems likely that the fifteen species present today are all that remain of a sometimes greater or sometimes lesser number of predecessors, many species having arisen and later become extinct since the original introduction of the genus into this continent.

Species formation has, I believe, resulted from effective spatial isolation. It is not difficult to imagine that during the geological past there were, as there are today, portions of the ranges of species in which populations are partially or altogether isolated. It is plain from the above studies that different genotypes may build up even in various parts of the more or less continuous range of a species, probably due to low vagility of the flies. Depending upon the degree of isolation, adaptive and non-adaptive changes that arise by mutation in such populations will be either slowly diffused into the genotype of the entire species or retained locally. Changes mixed into the genetic composition of the species as a whole may become lost completely or may persist as intraspecific variation. If locally occurring changes are advantageous (that is, have some small survival value), they may alter the entire parent species by outward diffusion from the place of origin, or, if long enough isolated, they may give rise to new species.

Differentiation of most of the existing species of *Dolichopeza* must have occurred at a time so remote that one could only speculate in general terms how or where it came about. If, however, one regards geographic races as incipient species, the case of *Dolichopeza polita* may be instructive. Much of the present range of this species lies in the area occupied by the last Pleistocene continental glacier; therefore, if the species existed at the time of that glacial advance, it must have been forced southward, into the Ozark Mountains, the central and southern Appalachian Mountains and part of the broad intervening lowland. If the habitats of the species have not changed appreciably, then the Ozark population (*polita pratti*) must have been rather effectively isolated by the lower Mississippi Valley, in which rock outcrops are not common; and the eastern and central populations probably were partially isolated on the eastern and western slopes of the Appalachians, respectively. Following the withdrawal of the glacier, the Ozark and central forms could have slowly made their way northward through the advancing forests, from one rocky or outcrop area to the next, not coming into contact until they reached north central Illinois. The central form (*polita cornuta*) maintained its subspecific relationship with *polita polita* along the Appalachian ridges but on reaching northern Ohio encountered representatives of the typical race moving westward from Pennsylvania, from which area the central form had long been isolated by the glacier. There the two forms reacted as full species. The eastern form, meanwhile, being less restricted to rocky habitats and proceeding from an unglaciated area much farther north than the other two, moved westward through the Great Lakes region until it encountered *polita cornuta* in Michigan and *polita pratti* in Wisconsin, in each case failing to interbreed and thus maintaining a specific degree of isolation. This interpretation is based upon present knowledge of distribution (see Map 6) and, of course, may need to be changed when further data are available.



244

FIG. 244. Diagram of supposed relationship of species and subspecies of the genus *Dolichopeza* in North America.

Interspecific relationships.—It seems likely that within the genus *Dolichopeza* certain adaptive structures have become well established and might be thought of as having reached a degree of stability as a result of close correlation of form with function. Stated another way, it may be that the genus must retain these characteristics in order to survive in its particular range of ecological niches. These characters common to all species of the genus may be said to be primitive for the genus, although they may be specialized in comparison to common characters of the family Tipulidae. Applying this same principle to the arrangement of species within the genus, widespread characters such as the pattern of wing venation may be regarded as primitive at the subgeneric level, or a certain kind of gonapophyses as primitive for a species group. Thus, the more characters any two species have in common, the more closely related they are judged to be. In attempting to arrange the species according to their most probable relationships (Fig. 244), I have used wherever possible characters least likely to have been directly influenced by environment. Hypopygial features, for example, have been found most useful, for I cannot perceive that the variations in shape of the ninth tergum, the dististyles or gonapophyses would be affected materially by a change in the species' environment. In contrast, coloration seems to be closely correlated with the type of habitat. On the basis of coloration, *subalbipes* would appear more closely related to *carolus* than to *johnsonella,* and *walleyi* more closely akin to *dorsalis* than to *sayi.* The various relationships indicated in Figure 244 are discussed in detail in the species accounts and need not be repeated here. Although this figure indicates no time scale, the levels of separation of lines of descent are intended to suggest relative lengths of time. The presence of most species both within and outside the area of the last Pleistocene glaciation suggests they have existed for approximately 10,000 years, at least. Lines of descent terminated by dashes are introduced to indicate supposed indirect derivation of one existing line from another. Lastly, considering only those characteristics of larvae and pupae used in this study for differentiating species, it appears that differences in the immature stages are of phylogenetic significance rather than adaptations to environment.

A brief hypothetical history of the genus Dolichopeza in North America.—The distribution of North American species of *Dolichopeza* indicates that they are a boreal and sub-boreal group, virtually limited to forested areas. In the Oligocene, the genus *Dolichopeza* may have been widely distributed in the northern parts of Europe, Asia and North America, for cool forests are thought to have been widespread in the northern continents, at that time. As a result of subsequent cooling of continental climates, this forest belt was displaced southward, carrying with it its fauna; and in early Miocene time, the genus *Dolichopeza* possibly occurred throughout much of its present North American range, as well as in much of the western part of the continent. With the renewed uplift of the present Rocky Mountains, during the Pliocene epoch, the western forests were widely obliterated, giving way to grasslands in the rain shadow area east of the mountains and being somewhat replaced in the far west by a new flora of conifers. *Dolichopeza,* now confined to the hemlock-hardwood and deciduous forests of eastern North America, was widely separated from the Asiatic stock. Advances and recessions of Pleistocene ice forced some components of the genus as far southward as the Gulf coast and probably caused fractions of the populations of various species to become isolated, giving rise to new forms. With the last retreat of the continental glaciers, most of the populations drifted northward into the newly developing forests, but some stayed behind in the more deeply-shaded swamps and cooler valleys of the South. As the land warmed and oak-hickory forests replaced the moister woodlands, fragments of the once widespread populations of *Dolichopeza* were left in the cool ravines and valleys of the Mississippi basin, together with relict stands of the hemlock-hardwood forest. Today, the stronghold of *Dolichopeza* is in the forests of the upper Great Lakes, St. Lawrence and New England regions, and in fragments of that forest extending southward along the crests of the Appalachian Mountains. From this area, some species have moved far northwestward through the subarctic spruce-fir forest, finding there environmental conditions adequate for their needs. Outside the spruce-fir and hemlock-hardwood forests, however, the present discontinuous pattern of distribution is, in a sense, a slowly fading ghost of what once was probably the center of concentration of the genus *Dolichopeza* in North America.

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